

ADAM URBANEK

AN ATTEMPT AT BIOLOGICAL INTERPRETATION
OF EVOLUTIONARY CHANGES IN GRAPTOLITE COLONIES

Abstract. — Problems of morphological organization in graptolite colonies are discussed and suggestions made as to the supposed genetic mechanisms of their evolution. The regular astogenetic succession of thecae is interpreted as an effect of *morphophysiological gradients*. The spreading of new thecal types in forms constituting successive evolutionary stages of a lineage are believed to be manifestations of the *penetrance* and *expressivity* of respective genetic factors.

I. INTRODUCTION

The attractiveness of graptolite studies seems to have been constantly increasing for some years past. Very probably this is due in a great measure to the publication of Kozłowski's excellent monograph (1948) establishing the systematic position of graptolites. This work is undoubtedly an important step towards the full grasping of the nature of graptolite colonies. Kozłowski's work completely re-orientated our views and is highly stimulating for further researches in that direction.

At present, the central problem for understanding graptolite evolution is the problem of organization of their colonies and the supposed mechanisms of their genetic changes. Thus far no publication has appeared dealing more at large with the above mentioned problems. The majority of papers so far published deal with more partial problems only, most particularly the morphological analysis of the various forms and their stratigraphic distribution. Hence, an attempt to utilize the assembled evidence in order to reveal broader aspects of the evolution of that group does not seem to be precocious.

The attempt here made to interpret the evolutionary processes in graptolite colonies is based not on palaeontological evidence only, but likewise on ascertained data and theories from the field of physiology, experimental embryology, and most particularly that of genetics. The writer's intention was to analyse the development and evolution of graptolite colonies in order to determine some more general laws

governing these processes. It has become apparent that these laws may be described in well known biological terms and concepts, and thus contribute to their explanation. The examination of fossil material from this aspect will in turn throw some light on a number of important questions linked with the genetic mechanism of evolution. The genetic method introduced into palaeontological studies in so excellent a manner by Simpson (1944, 1953) opens up new horizons for research work, and its use will prove of advantage in the study of numerous problems waiting to be solved by palaeontologists.

Unfortunately, the material available to the writer, as well as evidence thus far assembled by other graptolitologists, is not adequate enough for a description of the evolutionary processes in terms of population genetics. Our imperfect knowledge of the condition of environment in which graptolites lived and of environmental changes during the evolution of particular graptolite lineages, as well as our incomplete and merely hypothetical comprehension of the functional significance of the changing structures — all hamper an analysis of the selective and ecological mechanisms of these processes. Moreover, possibilities for interpretation are markedly restricted by lack of data concerning the most fundamental biological properties of graptolites, e.g. mode of their reproduction (self- or cross-fertilization?). However, it has been shown that the analysis of some of the better known processes from the aspect of physiological genetics and phenogenetics, as well as a comparison with the known morphogenetical regularities in living organisms, may lead to interesting inferences. Though this approach to the investigation of fossil materials is not perfectly new (comp. Swinnerton, 1932), still it represents a certain novelty in palaeontological literature, and the use of it has not thus far been adequate. In future, these investigations will, perhaps, be supplemented by the quantitative analysis, but even the present results seem distinctly interesting. The views just considered may naturally be regarded as a working hypothesis only and they will be subject to certain modifications in consequence of further studies. The writer ventures to hope, however, that they will constitute a base for further discussion on this interesting problem.

It is a pleasant duty of the writer to express his most sincere thanks to Professor Roman Kozłowski, Head of the Palaeozoological Institutes of the Polish Academy of Sciences and of the Warsaw University, for the kind interest and most valuable suggestions offered throughout the preparation of the present paper, also for reading the text and for most helpful critical comments.

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II. THE PRESENT STATUS OF THE PROBLEM AND THE PALAEOLOGICAL EVIDENCE

Evolution of animal colonies is one of the most interesting biological phenomena. The complex interrelations in the development of particular individuals in a colony (oozoid ontogeny, thecal blastogeny), development of the whole colony (astogeny i.e. cormogeny, also lateral branching i.e. cladogeny) and the phylogenetic changes of astogeny (evolution of the colonies) — give a good clue into the mutual interdependence of these processes. Unfortunately, neither the morphology nor the genetics of colonial animals have been adequately investigated. An exception here is the excellent study of Beklemišev (1950), concerning the colonies of Bilateria.

Graptolite evolution is one of the most striking examples of the evolution of colonial organisms. As compared with colonies of Pterobranchia which most probably come closest to them, graptolite colonies are distinguished by far greater degree of integration expressed by a definite structural pattern.

Comparison of graptolite colonies on a wider background of higher invertebrates shows that various stages of colonialism and the various stages in development of physiological relations between individuals may be there encountered (Beklemišev, 1950). Among pterobranchians, allied to graptolites, *Atubaria* is supposedly the only one really solitary organism which does not produce any swarm-like assemblages, common in numerous Cephalodiscidae (Sato, 1936). It is just from such forms that other forms might arise with a tendency to progressive colonialism. The formation of the clone itself — a group of individuals formed by asexual

reproduction from one parental individual, the founder of the clone — may be regarded as the most primitive stage of that process. That parental individual is usually a corresponding oozoid. The formation of the clone itself most likely constitutes the indispensable base for the development of more advanced colonialism. Moreover, in certain cases, the originating clone forms a short lived assemblage. This for some time surrounds the parental zooid, to be subsequently dispersed. Such assemblages of individuals occur e.g. in some of the Loxosomatidae (Kamptozoa). A somewhat more advanced stage of that process is represented by various species of *Cephalodiscus*, particularly by *Cephalodiscus (Demiothecia) gracilis* Harmer. The particular individuals, even though finally separating from the parent zooid, do not disperse but form stable assemblages and produce thecae united with the thecae of the oozoid. This results in a coenecium which is an assemblage of tubes containing the particular zooids forming a "pseudocolony" (Dawydoff, 1948). According to van der Horst (1939), owing to the lack of connection between tissues of the particular individuals, assemblages of this type correspond ecologically rather to communities of insects, e.g. those of wasps, than to colonies. Nevertheless such stable population-clones may be regarded as an initial process subsequently leading to the formation of true colonies in other pterobranchians and graptolites (Beklemišev, 1950). A similar or perhaps still more primitive stage of colonialism is represented by gregarious *Phoronis ovalis*. Their progeny produced by architomy grow within a tube which is the continuation of the tube of parental zooid, thus forming an assemblage of tubes occupied by individuals of the clone. Individuals making up such swarm-like assemblages have most likely in a certain way been integrated. This is suggested by the examination of similar "colonial populations" of insects (Alle, Emerson et al., 1950). One of the factors here is probably the coenecium, common to all individuals.

A still more advanced stage of colonialism would be represented by *Cephalodiscus (Demiothecia) sibogae* Harmer where individuals produced by budding remain interconnected and are believed not to be subsequently separated (van der Horst, 1939; Krumbach, 1937; Beklemišev, 1950). This type of colonies would not fundamentally differ from colonies of *Rhabdopleura* where individuals are produced by budding from the stolon to which they remain permanently attached. On the whole, relations here correspond to those in graptolite colonies (Dendroidea). Hence we may distinguish the following stages of colonialism:

1. Clone-like populations, supposedly constituting the indispensable genetic base for the further development of colonialism and the appearance of a certain stability of the formed assemblages.

2. Clones whose individuals form stabilized swarm-like assemblage: with a common coenecium (pseudocolonies).

3. Colonies consisting of individuals connected by common tissues which provide the indispensable base for further physiological integration of a colony (true colonies).

4. Further integration of colonies, among others expressed in a) reduced individuality of particular zooids, b) appearance of polymorphism, c) development of colonial organs and of cormidia.

The above mentioned stages of colonialism need not necessarily be all represented in evolution of all hemichordates. Moreover no adequate evidence exists indicating which group of hemichordates should be considered as ancestral for remaining ones. It is therefore possible that graptolite colonies may have been produced immediately by budding and the formation of a clone, whose individuals do not separate. In this latter case, stages 1-2 would be omitted.

Nevertheless, the numerous intergradations between a true colony and a typical population of solitary organisms consisting of physiologically more or less independent individuals, do not permit a sharp delimitation between these various organization types in conspecific individuals. Ecological data clearly indicate that a certain degree of integration and organization occurs in every population. Hence colonies would differ rather in the various quantitative expression of these properties whose evolutionary changes may have been gradual. Inasmuch as stages 1 and 2 may undoubtedly be regarded merely as a particular case of an ecological population, stage 3 may be considered as transient. Common genetic control and physiological regulation are here an expression of individual laws governing the colony as a unit; other phenomena, however, do not permit us to consider a graptolite colony as a single organism of higher order. This would be confirmed by the absence in graptolite colonies of such colonial organs as have been formed e.g. in Siphonophora. Neither has individual polymorphism been developed, so common in highly integrated colonies of Hydrozoa, Siphonophora and Bryozoa. Hence it would be incorrect to regard a graptolite colony as a simple organism of higher order, a super-individual whose separate zooids function as organs¹.

The peculiar organization of graptolite colonies may rather be interpreted as a certain organization of a group of individuals, i.e. as

¹ An exception here may be the pneumatophors, "the floating vesicles" of some graptolite colonies (synrhabdosomes), also an organ like the virgula, which may be regarded as colonial organs. But in this case too, they are more likely a product of the extra-thecal membrane of tissues, i.e. the analogue of caenosarc rather than individuals specialized to particular functions.

a particular type of ecological population. Physiological and genetical processes occurring in graptolite colonies may be considered either as individual or populationary. The former of these standpoints may appear particularly justified in relation to physiological integration and genetical control of colonies, while the latter is especially applicable in relation to evolutionary changes of the mode of astogeny (comp. p. 169). These changes do not occur simultaneously in all individuals within the colony, but are initially manifested in a part of them only. Hence evolution of a graptolite colony occurs through changes of ontogeny in the particular individuals and their groups within the colony.

The organization of a colony has thus far been most adequately ascertained in two graptolite groups: Dendroidea and Graptoloidea.

Dendroidea undoubtedly represent a lower evolutionary stage of graptolite colonies. Nevertheless, a dendroid colony was already a well integrated unit as is expressed by its structural pattern, realized by a definite mode of budding (the occurrence of triads, "Wiman rule"; Kozłowski, 1948). Moreover, dendroids are characterized by a regular, constantly dichotomous mode of branching, expressed in the occurrence of "zones of branching", especially well marked in *Dictyonema* Hall and Anisograptidae Bulman (Bulman, 1950, 1958). Two kinds of processes are readily observable in dendroids. According to the views advanced by Beklemišev (1950), they may be both regarded as expression of an advanced stage of colonialism: a) diminished individuality of zooids expressed by the morphological degradation of bizooids, and b) intensified individuality of colony expressed by a definite pattern of colonial structure suggesting the occurrence of a definite morphophysiological integration of the colony. The possible occurrence in graptolites of certain tendencies to produce a kind of cormidia are perhaps indicated by occurrence of triads and various other forms of a constant "thecal grouping", as e.g. the presence in *Acanthograptus* Spencer of a twig grouping of autothecae. However, these tendencies have never been realized on a scale comparable to that in Coelenterata.

It is in Graptoloidea that we encounter processes distinctly indicating that these graptolite colonies constitute an integrated unit to which the structure and the functions of particular individuals have been subordinated. In Dichograptidae Lapworth we may observe the significance of the structural pattern of the colony, which determines the number and the mode of lateral branching (Bulman, 1958). Another process may here be observed, that of the progressive size increase of the members of the colony, occurring on the particular branches in the course of astogeny. On the whole, the size of thecae increases with the

growing distance from the initial part of the colony, i.e. the sicula. In some graptoloids, however, especially in Phyllograpti, Tetragrapti and some Didymograpti, thecae secondarily decrease in size at the distal ends of rhabdosome. This phenomenon seems to be caused by corresponding growth relations of thecae on growing tips of particular stipes. A series of budding thecae on different growth stages, showing decrease in size, is always present at the growing end in young and more mature rhabdosomes. When, for some reasons, the growth stops, these growth relations seem to be responsible for size decrease of most distal thecae in certain Dichograptidae.

In higher Graptoloidea astogenetic changes are expressed not by the increase of thecal dimensions only, but moreover by accompanying changes in the shape, occasionally bearing a distinct character of allometric changes. Hence, certain morphological characters are either stressed or reduced, as e.g. in Diplograptidae. In *Diplograptus* McCoy the proximal thecae of the rhabdosome are ventrally strongly excavated; the median ones less conspicuously incised; the distal nearly straight. These changes take place by gradual modifications of thecal shape without any sharp morphological discontinuity.

Among the monograptids, however, these processes are expressed with strongest intensity. Forms occur here displaying strong differences of thecal structure within one colony so much so that proximal thecae differ notably from the distal. The term "biform" has been introduced by Elles and Wood (1901—1918) with reference to these monograptids. On analysing data available on astogenetic variability in graptoloids, particularly in Monograptidae which have been more thoroughly studied in this respect, we may confirm that it is expressed by gradual modifications in the successive thecae. Through a number of intermediate stages these modifications lead on to morphologically extreme types corresponding to the typical proximal and distal thecae. These changes most frequently involve the following characters (comp. fig. 1, 2).

A. *Size and shape of thecae*: size of thecae, length and width of protheca and of metatheca, length of protheca/length of metatheca ratio, shape of ventral wall, outline of thecal aperture, presence or absence of apertural processes and their size and shape, degree of bending of apertural region, overlap of thecae and the extent of their isolation, inclination angle of thecae to the axis of the rhabdosome, distance between thecae, mode of thecal budding, presence, degree of reduction or absence of periderm.

B. *Shape of the rhabdosome*: straight or provided with a variable ventral, dorsal or dorso-ventral curvature, with variable coiling either

planispiral or helicoidal, or coiling along the axis of the rhabdosome, branching frequency of stipes².

Doubtlessly, there is some interdependence between features of group A and group B, since the shape of the rhabdosome is occasionally in a certain sense determined by the structure of thecae and their succession. A striking example here is that of representatives of *Petalograptinae* (fig. 9) of which *Cephalograptus* Hopkinson is in Bulman's opinion (1955) "an extreme development of *Petalograptus*" (p. 87). This may be explained by the supposition that the foliate shape of the rhabdosome in *Petalograptus* Suess has experienced strong elongation in *Cephalograptus*. This has been effected by corresponding allometric modifications of thecae, with a bearing on changes in the shape of the whole colony.

Among some evolutionary lines of the monograptids, Sudbury (1958) has likewise been able to correlate the inclination angle of thecae or their isolation with the curvature of the rhabdosome. In *Monograptus argenteus* (Nicholson) e.g. the proximal thecae do not overlap at first, but do so rapidly after a certain distance, leading to strong local bending of the rhabdosome (Bulman, 1951; Sudbury, 1958). Similar relations have been ascertained in many other forms.

Taking into consideration data available on the astogenetic variability of thecae in Graptoloidea, and particularly so in monograptids, the following classification of colonies into groups, according to the type of their astogenetic succession, is proposed.

A. *Uniaxiate colonies* — with one only rhabdosome branch present.

1. Forms displaying the same thecal type throughout the rhabdosome: *uniform*; astogeny here is expressed by changes of size and some slight allometric effects only. Many representatives of the monograptids, among others of the genera *Monograptus* Geinitz and *Pristiograptus* Jaekel, are here referable: e.g. *Monograptus clingani* (Caruthers), *M. communis* (Lapworth), *M. uncinatus* Tullberg, *Pristiograptus dubius* (Suess) may be mentioned as those which have been more

² The changes which some of the just mentioned structural characters undergo, have been more closely investigated by biometric methods. Urbanek (1953) has attempted to analyse changes referring to height of rhabdosome and shape of aperture in *Saetograptus chimaera cervicornis* Urb.; Kraatz (1958) has thoroughly studied the astogenetic variability of a number of indices in a monograptid described by him as *Monograptus kallimorphus* Kraatz; measurements of thecal size in some monograptids without overlap and their analysis were also made by Sudbury (1958).

Fig. 1. — Astogenetic succession of thecae in various Monograptidae: A *Monograptus argenteus* (Nicholson), B *M. fimbriatus* (Nicholson), C *M. raitzhainiensis* (Eisel), D *M. triangulatus* (Harkness), E *M. communis* (Lapworth); outline of rhabdosomes approx. $\times 2$, thecae approx. $\times 10$, fusellar structure simplified (from Bulman, 1951, 1958).

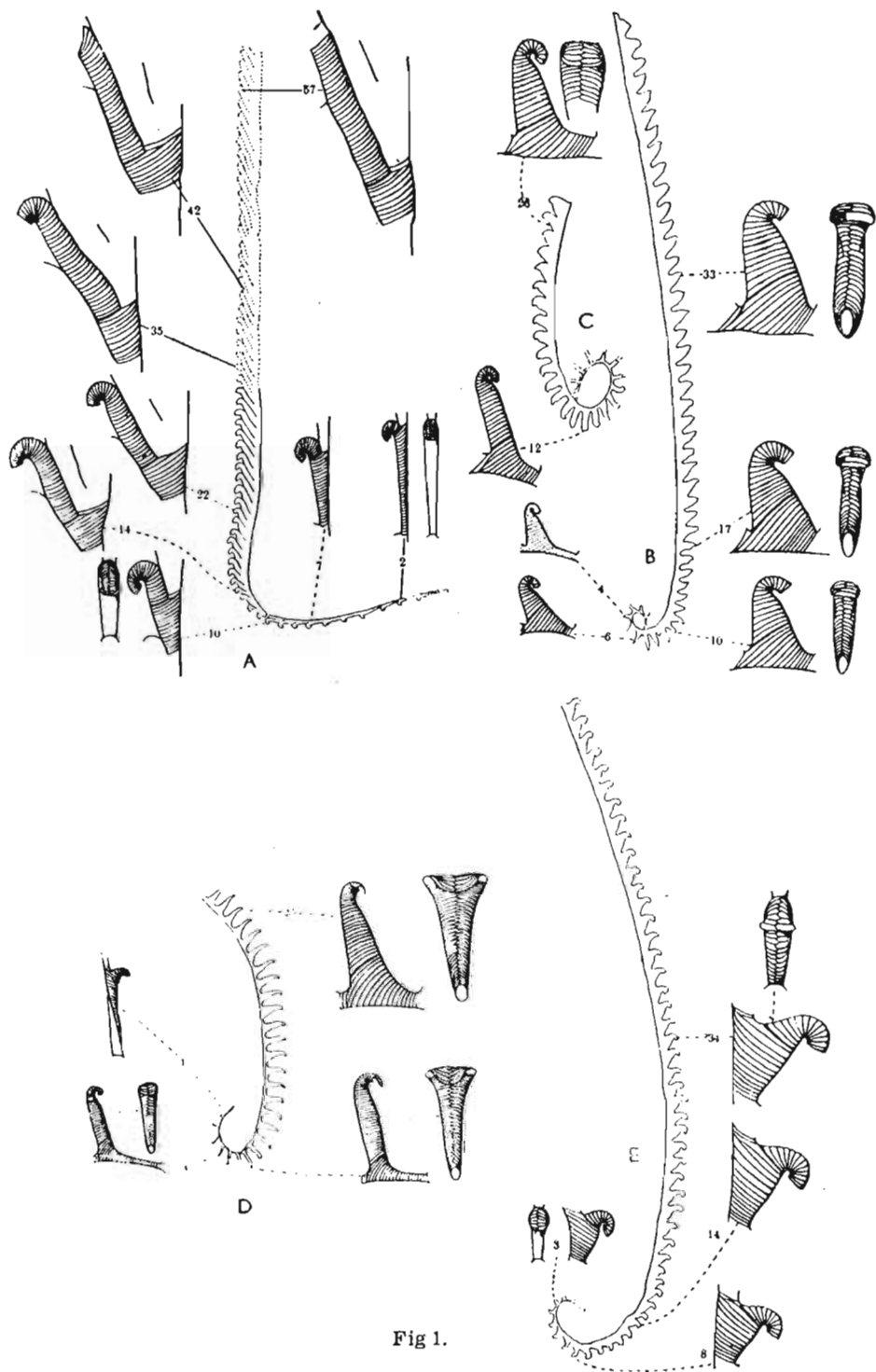


Fig 1.

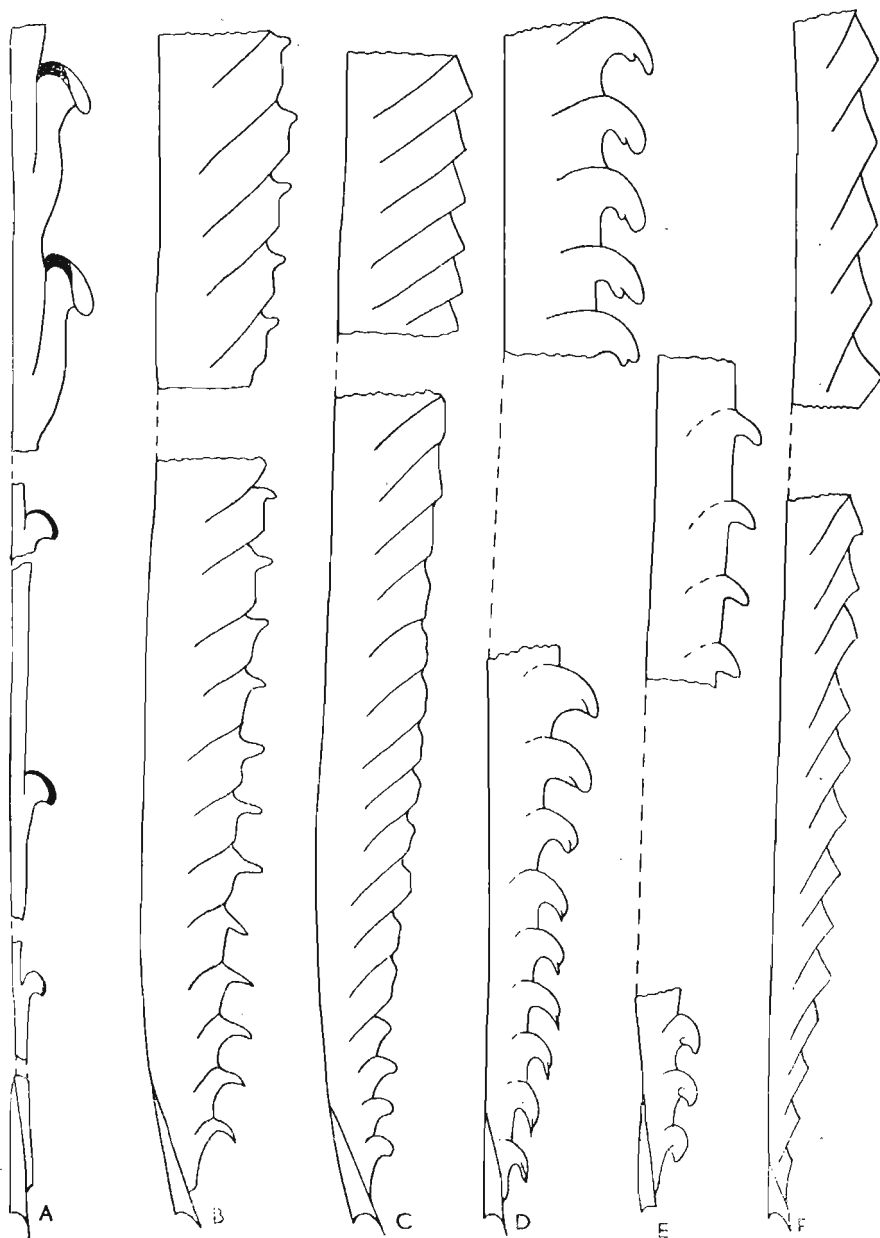


Fig. 2. — Astogenetic succession of thecae in various Monograptidae, based on specimens dissolved out of their matrix: A *Cucullograptus hemiaversus* n.sp., B *Saetograptus chimaera* (Barrande), C *Colonograptus colonus* (Barrande), D *Monograptus priodon* (Bronn), E *M. uncinatus* Tullberg, F *Pristiograptus dubius* (Suess). For each species proximal, medial and distal thecae are shown. From various Silurian erratic boulders. A approx. $\times 20$, B-F approx. $\times 10$.

fully investigated in this respect. Forms of this type are shown in fig. 1 E, 2 E, F).

2. Forms whose proximal thecae differ distinctly from the distal ones: *biform*. Two types of astogenetic succession may be here distinguished:

a) forms whose proximal thecae are distinguished by additional characters not present in distal thecae, or by more intense manifestation of some characters less marked in distal thecae. This group comprises very numerous forms: out of monograptids, many representatives of *Monograptus* Geinitz³, *Colonograptus* Přibyl, *Saetograptus* Přibyl; e.g. species *Monograptus revolutus* (Kurck), *M. argenteus* (Nicholson), *M. difformis* Törnquist, *M. triangulatus* (Harkness), to a certain extent also *Monograptus priodon* (Bronn), *Colonograptus colonus* (Barrande) and *Saetograptus chimaera* (Barrande). Forms of this group are represented in fig. 1 A-D, 2 B-D;

b) forms whose distal thecae are distinguished by some additional characters not occurring in proximal thecae, or by stronger intensity of manifestation of certain characters. Thus far these forms have not been adequately known. The present writer has, however, ascertained the occurrence of a form representing that type of astogenetic succession (comp. fig. 2 A) for which he suggests the name of *Cucullograptus hemiaversus* n.sp.⁴

B. *Multiaxiate colonies* — colonies with more than one branch.

1. Forms lacking differences in astogenetic succession on the main and lateral branches, so that the colony is apparently an assemblage of virtually independent uniaxiate colonies: *Dichograptidae*, *Leptograptidae*, *Diversograptus* Manck, *Limograptus* Frech, *Abiesgraptus* Hundt.

2. Forms displaying differences of astogenetic succession on the main branch and on the lateral branches: *Cyrtograptus* Carruthers (comp. fig. 10).

Elles (1922) was the first to give an interpretation of the interesting phenomenon of astogenetic variability of thecae, particularly as it is expressed in "biform" graptolites. According to her hypothesis, "biformism" is a consequence of the particular mode of evolution of graptolite colonies⁵. In Elles' opinion, biformism is an effect of the

³ Numerous species of *Monograptus* distinguished by considerable degree of biformism have been separated into the genera *Demirastrites* Eisel and *Pernero-graptus* Přibyl. This problem is discussed on p. 207.

⁴ Forms mentioned in the text as new species or subspecies are described in an appendix attached to the present paper (see p. 211).

⁵ The views here stated have not all been "explicitly" expressed by Elles, but may be deduced from examples cited by that author.

phylogenetic changes in a colony. They occur rather through changes of individuals in a part of the colony than by simultaneous modifications in all members of one colony. In certain cases new features are believed

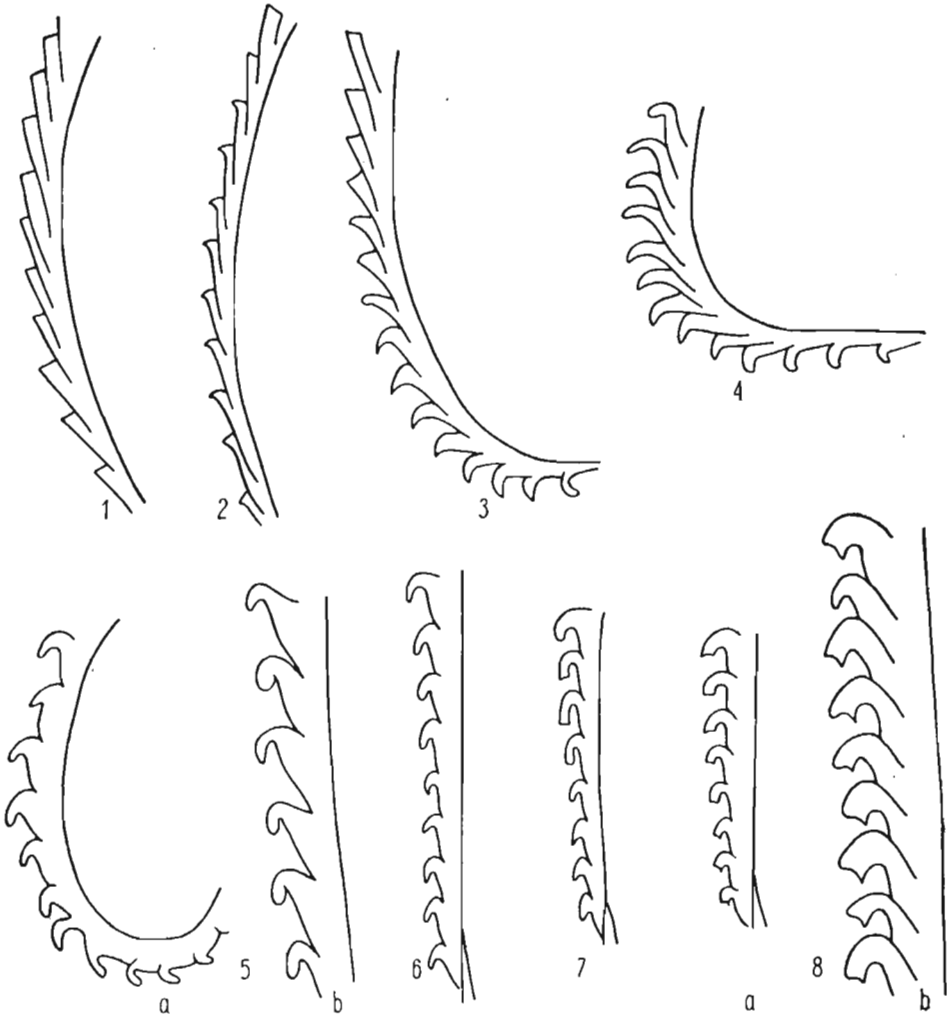


Fig. 3. — Supposed evolutionary trend in certain Monograptidae illustrating the "progressive series" in the sense of Elles. Development and spreading of hooked type of thecae (1-8); a proximal, b distal parts of rhabdosome (from Elles, 1922; redrawn with some modifications).

to be first introduced into the proximal part of the colony. According to Elles, this takes place when new progressive morphological features are introduced ("progressive series"). In these phylogenetic series we would be dealing with the gradual spreading of new features, progressively involving an increasing number of individuals of a colony and

finally spreading over the whole colony. An illustration of such a series is provided by the evolutionary line of monograpti which was believed by Elles to represent the successive stages of the spreading of the hooked thecal aperture (fig. 3)⁶. The process of morphological simplification, "the retrogressive series" is believed to occur according to another mode. The new character, morphologically constituting a simplification or reduction of the ancestral type of thecae, would then first appear

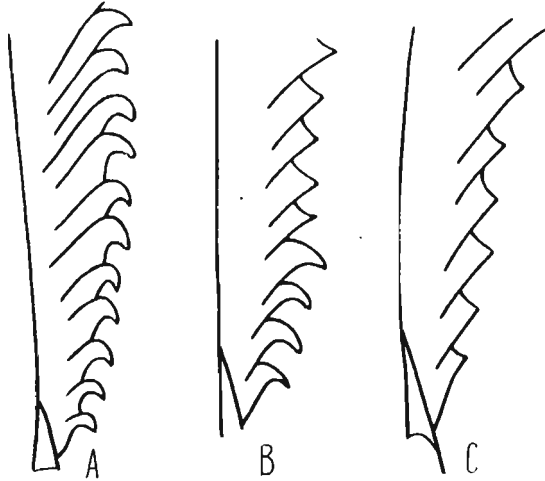


Fig. 4. Supposed evolutionary trend in Monograptidae leading from forms provided with hooked thecae (A) to forms with simple thecae (C) illustrating the "retrogressive series" in the sense of Elles (from Elles, 1922; redrawn with some modifications).

in thecae of the distal part of the rhabdosome, subsequently — in a line of successive generations — involving the whole of the colony. The various "retrogressive lines from hook" (fig. 4) postulated by Elles are examples of these processes.

Of particular importance is here the fact, for the first time stressed by Elles, that in graptolites changes of thecal type occur by gradual spreading of the new thecal type within colonies which constitute the successive stages of given phylogenetic series. These concepts were subsequently confirmed in papers by other authors, particularly those of

⁶ It seems that the phylogenetic series suggested by Elles does not constitute one evolutionary trend. In other words, it is not an unbroken chain of the direct ancestors and descendants of one stock (O. Abel's "Ahnenreihe"), but supposedly merely represents the successive morphological stages occurring during the evolution in a number of such trends (O. Abel's "Stufenreihe"). The occurrence of some "retrogressive series" are confirmed recently by Sudbury (1958), but the "retrogressive" series, postulated by Elles and quoted below to illustrate her considerations, seems rather doubtful in some respects.

Bulman (1933, 1951, 1958) and Sudbury (1958) who published new and reliable evidence to support them. Jaeger (1959) also described phenomena of gradual development of apertural lobes in the geologically youngest monograptids (ey' beds). He has arrived at the conclusion that in some of lineages distinguished by him, this character was initially manifested in proximal parts of the rhabdosome, subsequently spreading toward the distal end. This mode of evolution was determined by Jaeger as a proterogeny. The opinion advanced by Elles that changes in thecae are realized by the gradual spreading of a new thecal type along the rhabdosome seems, therefore, sufficiently sound, while her other views call for further discussion.

In considering these facts, de Beer (1958 and earlier) attempted to explain them from the embryological standpoint. He believed that some modes of the introduction and distribution of new features in graptolite colonies might be regarded as a case of "colonial neoteny" (1958, p. 86—87). By using certain analogies we might indeed suggest here a sort of proterogeny, paedomorphosis or colonial gerontomorphosis. However, a deeper insight into the problem shows that in respect to features "introduced proximally", the "colonial paedomorphosis" would be expressed by changes affecting particular individuals and bearing a distinctly gerontomorphic character. For example, in the spreading of the "hooked" shape distal thecae acquire mature or gerontic characters of proximal thecae of their ancestors. Hence it seems that concepts applicable to individual ontogeny, when used in reference to colonial development realized by changes of numerous individuals, may lead to misunderstandings and will not clear up any doubts. Bulman is thus right in asserting that "concepts borrowed from simple ontogenies may become misleading when applied to astogeny" (1951, p. 327).

The interesting and important hypothesis advanced by Elles is actually more a description of certain facts than an analysis of the supposed causes of these facts. Hence Westoll's hypothesis (1950) attempting a causal explanation of these processes is of marked interest. Grounding his considerations on de Beer's views (1940, 1958), Westoll advanced his "potential hypermorph" concept⁷. He used it in trying to explain the probable evolutionary mechanism of certain monograptids which had by Elles been referred to the progressive and retrogressive series.

⁷ According to de Beer's terminology (1940, 1945), hypermorphism may be defined as a phylogenetic process consisting in the addition of a new stage to the adult stage of the ancestor (A. N. Severtzoff's *anaboly, prolongation* of V. Franz). Westoll's (1950) potential hypermorphosis may be defined as a state when corresponding morphological modifications might be realized through the addition of a new stage of ontogeny, but do not actually occur owing to restricted growth ability.

According to Westoll, certain features of thecal structure might be connected with a definite stage of thecal growth or of development attained by the theca. During the evolution of the "progressive series" in the various forms, the number of zooids attaining that growth stage would progressively increase (comp. fig. 5: *argenteus* — *prionon*). During the colonial evolution of graptolites belonging to the "retrogressive series", proximal individuals only would attain a stage of growth in which appropriate apertural differentiation occurs. The other members of the colony not having attained that stage would — morphologically speaking — be simplified owing to relative growth inhibition. The evolution of the retrogressive series (comp. fig. 5: *prionon* — cf. *colonus*) would consist just of these changes constituting an abbreviation of ontogeny, i.e. a sort of neoteny. The changes may likewise be according to Westoll, "stated in terms of de Beer's paedomorphosis and retardation".

Westoll's views were met by criticism on the part of Bulman (1951). He demonstrated that they do not adequately explain all the cases of colonial evolution in monograpti. In Bulman's opinion, they are not, in the first place, applicable to those processes during the introduction and spreading of new progressive thecal types (Elles' progressive series). The "potential hypermorph" concept accepts the existence of stadial differences between the members of one colony due to absence of a well developed terminal segment in thecae with simple apertural parts. According to Bulman, this is not very likely since it does not agree with the fact that all individuals of a colony invariably represent the same thecal segment, i.e. the metatheca. It is to Bulman too, that we owe the detailed analysis of astogenetic changes of thecal shape in a number of monograpti which represent the various stages of certain phylogenetic series (fig. 1). In some of these Bulman has ascertained the well known fact that proximal thecae are morphologically more

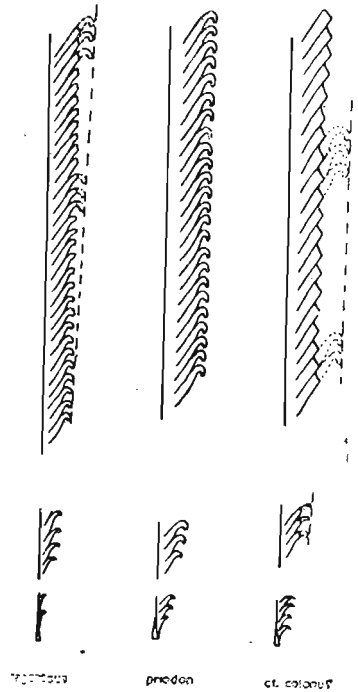


Fig. 5. — Diagram illustrating the spreading and loss of hooked thecae in "progressive" and "retrogressive" series in monograptids, according to the "potential hypermorph concept" of Westoll. Hooked shape of aperture is believed to be linked with a defined growth stage of theca (marked by broken line), which in some species — may be attained by all individuals of a colony, in others only by part of them (from Westoll, 1950).

strongly modified than the distal. In *Monograptus decipiens* Törnquist and *M. communis* (Lapworth) that author has observed, however, that "new features may originate or be dominantly expressed distally, but an appearance limited to the proximal end is far more common". Bulman's investigations have made important progress in the analysis of the mode of thecal variation in some monograptids and contribute to the comprehension of a graptolite colony as a unit under common genetic control. In result of his considerations, Bulman (1951, 1958) is inclined to accept the "orthodox view that the new types are transformations of thecal form introduced proximally into the rhabdosome with the corollary that the fact concerned loses its potency as the colony ages" (1951). Bulman believes that hypermorphosis might possibly explain the "retrogressive hook series" (1951), but that the occurrence here "of some factor of gradually decreasing intensity throughout the colonial unit appears a more probable explanation" (1958). According to that author (1958), the "succession of individuals, appears as something comparable with the varying field of growth potential of a solitary organism and perhaps finds its closest parallel among metamERICALLY segmented animals".

Westoll's views were criticized by Urbanek (1958) from another standpoint, based on his retrogressive series concept. Westoll agrees with the hypothesis of Elles that the "retrogressive series" would lead from uniform forms provided with hooked thecae throughout the length of the rhabdosome to forms with hooked thecae limited to the proximal part of the rhabdosome. Now, however, we know that the phylogenetic trend suggested by Elles requires certain amendments, since ancestors of this series too, i. e. *Monograptus priodon* (Bronn) are likewise characterized by some degree of biformism. In the just named form the lateral processes of proximal thecae differ strongly from those of distal thecae and, in spite of the uniform character of the apertural lobes throughout the rhabdosome length, this is undoubtedly a representative of the "biform" type (comp. fig. 2 D). Hence, within the suggested evolutionary trend we would not be dealing with an appearance of biformism but with differences between ancestors and descendants, consisting in the absence or presence of apertural lobes. Hence, this example, neglecting even some uncertainties whether it may be considered as ancestral for the mentioned lineage, is not an illustration of Westoll's hypothesis, since within the suggested evolutionary trend the mode of evolution would undoubtedly differ from that supposed by that author.

Urbanek (1958, p. 28) has likewise stressed the strong similarities of the regular astogenetic succession of thecae in graptolite colonies

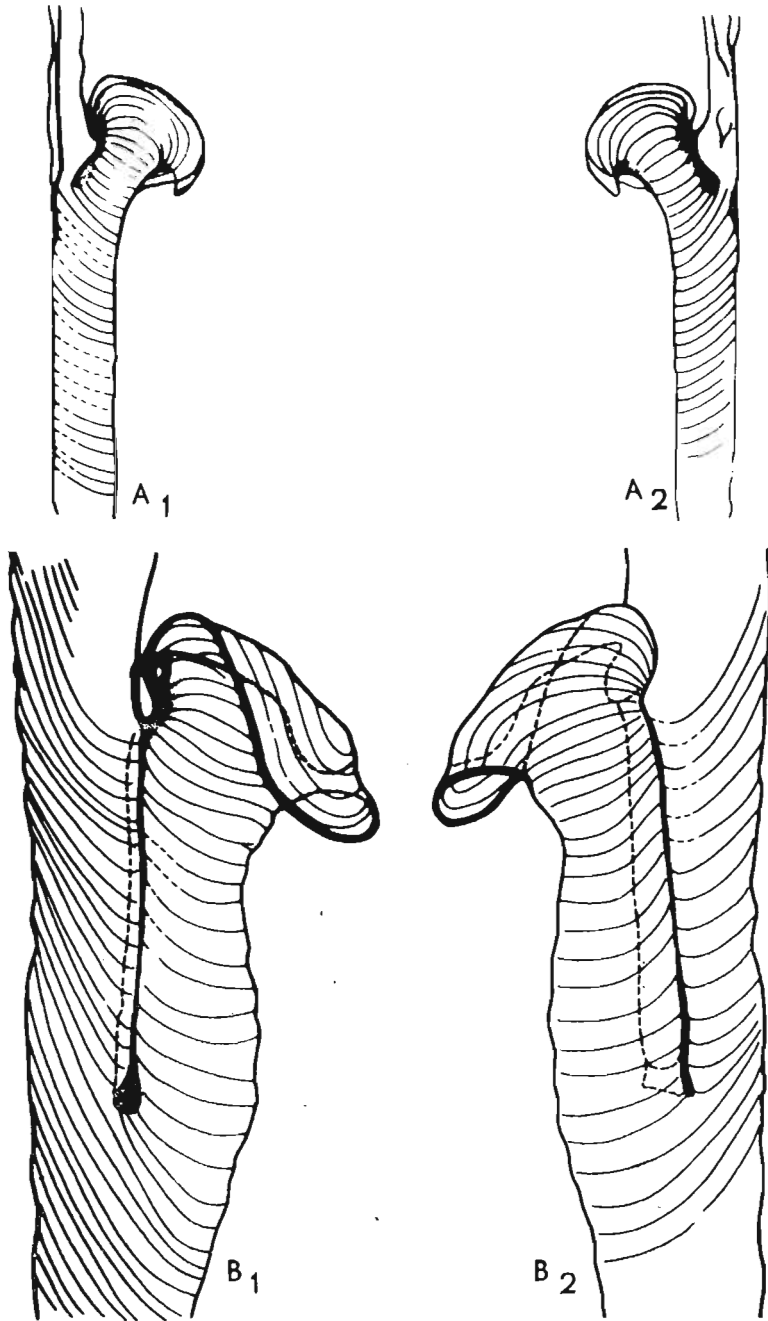


Fig. 6. — Fusellar structure of thecae in *Cucullograptus hemiaversus* n.sp. A_1 - A_2 proximal theca from right and left side, B_1 - B_2 distal theca from right and left side (boulder S. 200, (Rewal), approx. $\times 75$).

with the occurrence of "growth gradients" and the "growth gradients potential" concept, such as has recently been postulated by Huxley (1950). On the other hand, he has also pointed out difficulties encountered in the determination of the nature of stimulating and inhibiting factors, controlling the spreading of characters and moreover in the determination of factors responsible for thecal shape. According to Huxley's growth gradients theory, the decisive factor here would be the position of theca within the rhabdosome, while Bulman's considerations suggest rather the colonial age factor.

New light has been shed on the here studied problems by data resulting from the present writer's new investigations of regularities in the evolution of some Silurian graptolites from the Monograptidae, subfamily Cucullograptinae (Urbanek, 1958). These forms have been studied mainly from erratic boulders of Scandinavian origin, Ludlovian in age (comp. p. 176).

A new species, which the writer proposes to call *Cucullograptus hemiaversus* n. sp., displays a very peculiar structure. The thecae of this species are provided with two lateral apertural lobes, initially nearly symmetric. The subsequent thecae are characterized by progressive hypertrophy of the left lobe, accompanied by corresponding distrophy of the right one. Consequently, the more distal thecae display stronger asymmetry (fig. 2 A & 6). These forms may be, on existing evidence, traced to ancestors with two symmetric apertural lobes in thecae throughout the rhabdosome length. The just mentioned forms though not very abundant, are encountered within the graptolite fauna of erratic boulders (comp. p. 179). The hypertrophy of the left lobe in this evolutionary trend and its overlap onto the right lobe, as well as the associated distrophy of the right lobe, are all features "introduced distally" in a series of descendants. In a strictly morphological sense, the hypertrophy of the lobe and the appearance of asymmetry cannot be recognized as a retrogressive character responsible for structural simplification. On the contrary, we are more probably dealing here with progressive modification of the apertural apparatus. This is most distinctly shown in a form, by the writer named *Cucullograptus aversus rostratus* n. subsp.; it is referable to the same evolutionary trend. In the latter form, the left lobe shows further progressive development (com. p. 182). However, this feature, at first affecting the distal thecae alone (*C. hemiaversus* n. sp.), subsequently occurs throughout the rhabdosome (*C. aversus* (Eisenack)), hence behaving as new features in Elles' "retrogressive series".

Bulman is in favour of a similar conclusion when he writes: "some evidence, however, indicates that the thecal changes affect the distal

part of the rhabdosome alone, and in *Cyrtograptus* the more conspicuous changes commonly appear to be in the distal thecae" (1955, p. 45).

Thorsteinsson's data (1955) likewise apparently suggest that "throughout the cyrtograptids the proximal thecae are invariably of a closely comparable type, and that differences appearing in the distal thecae cannot be classed exactly as retrogressive" (*vide* Bulman, 1955, p. 49).

On the other hand, Sudbury (1958) found that the simplification of rastritiform thecae in the lineage of *Monograptus triangulatus fimbriatus* (Nich.) is a character introduced distally into the rhabdosome. This means that the mentioned mode of introduction of new characters is evidently independent of nature of the change being in some cases "progressive", in others "regressive" in the formally morphological sense.

Hence the distinction, proposed by Elles of the "progressive and retrogressive series" on differences in mode of introduction of new characters, is believed as unconfirmable with the evidence now available and hence it requires amendments. Therefore, group A, 2a of monograptids distinguished previously (comp. p. 137) comprises all forms with stronger modifications in the proximal parts of the rhabdosome, and their separation into representatives of the progressive and the retrogressive series does not seem reasonably justified. The last mentioned view is based on definite phylogenetic hypotheses which in turn call for some sound evidence. Should we discard this criterion, the distinction between "progressive" and "retrogressive" characters will lose its poignancy or perhaps be altogether impossible. Moreover, we are now in possession of evidence indicating that "progressive" characters may behave similarly as "regressive" characters should do according to the opinion of Elles.

Stronger manifestation of certain morphological characters in the distal part of the rhabdosome bars the supposition that astogenetic variability may be due to the aging of the colony as a whole, i. e. determined by the time and succession of budding of particular zooids. Distal zooids do not at all display lack of capacity for differentiation, and in some cases on the contrary they represent maximum structural modifications.

Cucullograptus hemiaversus n. sp. and its relatives moreover indicate that neither can Westoll's "potential hypermorph" concept be used to explain the evolution of this phylogenetic trend. Even though strong modifications have affected the apertural apparatus, they cannot be referred to lack or addition of certain growth stages or absence of certain thecal segments. Every morphological change of the peridermal structure in graptolites does indeed lead to growth changes (formation

or reduction of fuselli), similarly as in the case of the "accretionary type of growth" (Huxley, 1932), bearing an additive character. In this particular case, however, we may be all the more certain that morphological differences of adjacent thecae cannot be explained by growth

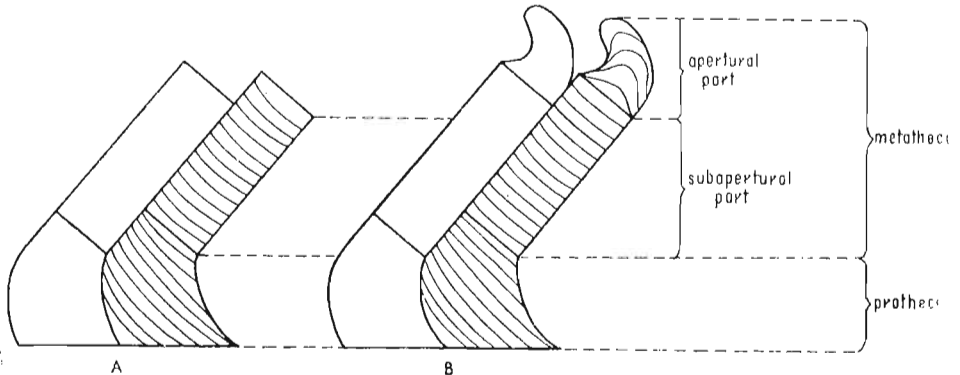


Fig. 7. — Comparison of homologous segments of thecae in Graptoloidea. Metatheca in graptoloids without apertural apparatus represents mere subapertural segment (A); metatheca in graptoloids provided with apertural apparatus represents both subapertural and apertural segments (B).

differences. In *Cucullograptus hemiaversus* n. sp. the thecae represent indeed not only the same thecal segment (metatheca) but, moreover, its apertural part is represented by apertural lobes developed in all the thecae. Hence it is doubtless that they represent the same growth stage, which would not necessarily always be so, if some thecae represent the subapertural part of metatheca alone (comp. fig. 7 A), while others the apertural one too (comp. fig. 7 B). Therefore, in the case of *C. hemiaversus* n. sp. growth differences of the various thecae, doubtlessly representing the same growth stage but nevertheless differing strongly, could not be the decisive factor determining the structure of the apertural apparatus. These differences do not consist in the absence or presence of the respective thecal segment (i. e. the apertural segment), but in various modifications of structure of the same segment.

Growth differences, as suggested by Westoll, doubtlessly occur in many cases, but his interpretation does not seem adequate for some other ones.

The above remarks might well be supplemented by stressing that Westoll's hypothesis, like all previously mentioned concepts, fails to interpret another important process, namely that of the changing expressivity of given characters, thanks to which evolution in graptolite colonies involves not only the spreading of a given character among the members of a colony, but changes of its expressivity too. The

particular stages of the "progressive series" differ not only in the number of thecae displaying a given character, but also in the degree of its expression (comp. also data of Bulman, 1951, Sudbury, 1958; see p. 175 of the present paper). On the other hand, the occurrence of regular growth differences in thecae of the rhabdosome, suggested by Westoll, would necessarily lead to the acceptance of growth gradients, and this has not been sufficiently taken into the account by Westoll.

On the basis of the above considerations, the present writer concludes that so far advanced concepts do not now adequately explain the available evidence which indicates that:

1) thecae may display regular morphological succession on the rhabdosome and these changes may consist either in the presence or absence of respective thecal segments, and also in different structural modifications of the same segment;

2) evolutionary changes may initially affect the proximal or the distal part alone, independently however of their being "progressive" or "regressive" features in the formally morphological sense;

3) in many graptolite groups evolution consists in gradual spreading of the new thecal type which may finally be manifested in all the members of the colony.

These considerations have induced the writer to search for a more general concept which would explain all colonial organization types thus far known in graptolites, and would be based on modern views concerning the process of integration and biological correlations and on up to date genetic views. In the discussion that now follows the writer has availed himself of numerous analogies taken from the study of living animals and plants, whenever the basic mechanism of these processes presented reasonable similarities.⁸

III. MORPHOPHYSIOLOGICAL INTERPRETATION OF ORGANIZATION OF GRAPTOLITE COLONIES

Organization of uniaxiate colonies

The presence in higher Graptoloidea colonies of an integrated morphological organization, expressed by a definite astogenetic succes-

⁸ The mode of evolutionary changes in graptolite colonies, realized primarily by change of a part of the colony, implies some analogy to the genomorph concept of Lang and Smith, and other authors, based on studies on colonial Tetracorallia. This interesting conception is, however, in many respects vague and indefinite, and this is why no comparison is made here with evolutionary changes in graptolite colonies — far more regular and better known (comp. Bulman, 1951).

sion, suggests some striking biological analogies. The gradual modification of thecae during astogeny in graptolite colonies of the "biform" type, leading to conspicuous differences between the proximal and distal thecae, doubtlessly indicates that in morphophysiological respect the graptolite colonies were characterized by peculiar polarity and that they were organized according to an "axiate pattern" (Child, 1941). During astogeny, thecal changes were manifested in small structural intergradations of adjacent individuals, without any morphological discontinuity and displaying a definite succession, i. e. direction of changes. These changes were so gradual that it is really never possible sharply to delimit the particular regions of the rhabdosome (comp. fig. 1, 2). Hence we may without hesitation accept *the appearance in such graptolite colonies of definite morphophysiological gradients*. We are namely dealing here with regular modifications of properties of individuals depending on their position in the colony. These facts seem quite closely to coincide with numerous biological processes which Child (1915, 1941) attempted to explain by his physiological gradient theory. The fundamental points of that gradient theory have, in one way or another, been recognized by a number of authors engaged in the study of the various branches of biology. They were i. a. D'Arcy Thompson (1952), Hörstadius (1935, and later works), Huxley (1932, 1950), Huxley and de Beer (1934), Runnström (1928, and later works), Spemann (1936, and earlier works).

Numerous authors have introduced certain amendments into that theory. Although Child asserted that the physiological gradients are expressed by the metabolic activity gradient, i. e. the respiratory gradient, it has never been possible to prove this, on the contrary, data are now available showing that in this respect the "dominant region" does not differ from the surrounding tissues (Needham, 1931, *vide* 1942; Huxley, 1932; Poležaiev, 1945). Moreover, there is considerable evidence indicating that the occurrence of gradients is associated with a corresponding mode of the production and distribution of morphogenetic substances. The physiological dominance in coelenterate colonies is even regarded by Barth (1940) and Spiegelman (1945) as competition for physiologically necessary substances (Spiegelman's "concept of physiological competition"). The gradual exhaustion of the still available amount of that substance may, in Waddington's opinion (1956), be responsible for the appearance of physiological gradients. This is the conclusion to be drawn from Spiegelman's (1945) and Waddington's (1956) considerations expressed in mathematical language (comp. also Tardent, 1956; Tardent & Tardent, 1956; Tardent & Eymann, 1959; Tweedell, 1958).

The presence in graptolite colonies of a distinct morphological gradient likewise seems to suggest that its origin is due to the spreading of appropriate morphogenetic factors. These are in most cases known in living organisms, represented by certain substances. Numerous experiments carried out on coelenterates seem to indicate that the dominance and physiological gradients may be due to the spreading of suitable substances. The blocking or restriction of inhibition has been here obtained by introducing into the coenosarcal cavity of a drop of oil, or air vesicles, or by ligation of the stolon (e. g. Barth, 1938). These mechanical factors check the spreading along the stolon of corresponding substances at the same time blocking the dominance (inhibition), (Spiegelman, 1945). In view of these facts it may be accepted that, within graptolite colonies, the gradient of such active substances would affect not some physiological properties only, but the morphogenetic too. Hence it seems that the interpretation of graptolite colonies by the "concept of physiological competition" is more reasonable than the acceptance of the "specific inhibition" concept, recently advanced by Rose (1957)⁹.

Independently of these discussions the occurrence of morphophysiological gradients has now been ascertained beyond any doubt (Huxley, 1932, 1950; Poležaiev, 1945; Wagner & Mitchell, 1955). The majority of authors agree that Child's hypothesis is a most creative and fruitful one. The fundamental points of the morphophysiological gradient theory (Child, 1915, 1941) are very helpful in interpreting the organization of graptolite colonies¹⁰. Without going into details of no bearing for our problems these points may be summarized as follows:

1. Both in solitary organisms and in colonies, gradual and directional changes of physiological and morphological properties are manifested, i. e. the occurrence of graded decrease, from the region of the highest

⁹ This hypothesis postulates that the cells of an organism are all provided with equal development abilities. Some of them, however, upon attaining suitable differentiation, will — by way of inhibition — prevent same differentiation processes, in others thus causing the remaining cells to take up a different direction of differentiation. The inhibiting factors are manifested by the direct contact of cells, by way of transmission of some surface changes. This hypothesis contains new and important ideas. They are, however, of greater significance with reference to organogeny than to astogeny (formation of colonies). E. g. it does not adequately explain the astogenetic succession of "uniform" graptolites, such as those provided with same differentiation, e. g. hooked thecae throughout the rhabdosome length. Neither does it seem justifiable to postulate that the direct surface contact of cells is the main way of the transmission of induction (inhibition) in graptolite colonies. Also the new concept of morphogenetic fields, based on spatial distribution of successive stages of a common chain of metabolic reactions, postulated by Abeloos (1955) for interpretation of regeneration phenomena in annelids, seems to be in a lesser degree applicable to graptolite colonies than the orthodox physiological gradient concept of Child.

¹⁰ See next page.

intensity to the region or regions of lowest intensity (gradients) is noted.

2. Individual or colonial integration is realized by control or dominance of certain centres over the remaining ones.

3. Physiological dominance or induction is realized by transport of certain chemical substances, or by transmission of energy changes¹¹ from centres physiologically dominant to those of lower intensity.

4. In many organisms the effectiveness of dominance decreases with increase in distance from a given region to the physiologically dominant centre.

5. The physiological isolation (isolation from control) of the different parts of solitary organisms or colonies varies in connection with the varying effectiveness of dominant (inducing) factors.

6. The varying range of physiological isolation determines the physiological and morphological properties in the given part of an individual or of a colony.

The organization of higher Graptoloidea colonies, particularly those of biform type, may be readily explained by application of the theory of morphophysiological gradients.

The regular astogenetic succession in "biform" graptolites suggests the presence in their colonies of peculiar morphophysiological gradients. In result of gradual modifications, distal thecae differ distinctly from the proximal, indicating certain *polarity* within graptolite colonies. This polarity, similarly as the polarity in living organisms, must have been associated with the presence of an inducing region. According to the linear nature of graptolite colonies, this inducing centre may be searched for in two regions of the colony, i. e. a) the proximal end (sicular region), or b) the distal end (budding end of the stolon). A consideration of these alternatives indicates that in graptolite colonies

¹⁰ In his considerations the present writer uses the term "morphophysiological gradient" to supplement the classical meaning given to it by Child when speaking about "physiological gradients". The idea of the "morphogenetic field", dwelt upon in several papers by Gurwitsch, Weiss, and Huxley & de Beer, does not necessarily seem applicable to graptolite colonies. "Morphogenetic fields" result from gradients (Child, 1941) and, in spite of certain suggestions, they cannot be regarded as a phenomenon independent of the gradient (comp. also Spiegelman, 1945). However, in many cases, these ideas are not accurately defined, being vague and indefinite (comp. also Poležaiev, 1945, Spiegelman, 1945), even though they keep up with the spirit of time (physical approach). Therefore, the classical biological meaning of the term "gradient", considerably less ambiguous, is here perfectly sufficient.

¹¹ The transmission of energy changes, interpreted by Child (1941) as transmission of mechanical, thermal or electrical changes, and, in the first place, that of nervous excitation, is not here discussed, since these factors could not in any important measure be responsible for the morphogenetic changes observed in graptolite colonies.

it is the sicular region, or rather the siculozoid, that may with most likelihood be recognized as the inducing region. In this connection the organization of graptolite colonies would correspond to that in the basipetal type of colonies of various athecate hydroids where the oldest zooid would be the centre of physiological dominance. Indeed, in most graptolites the siculae are of notably constant shape and, with a few exceptions, they were scarcely affected by any important morphological changes. This constancy in the shape and structure of siculae contrasts with the plasticity of thecae of all blastozoids in higher graptolite colonies. The morphological difference between the sicula, i.e. the prime theca of the colony and the next thecae, is considerably stronger than that between the adjacent thecae of the remaining portion of the rhabdosome. This gives rise to an analogy between the organization centre and the reacting tissues during individual development of animal organisms. In graptolite colonies the biological function of the former factor would be performed by the siculozoid, while the latter would be represented by the remaining zooids of the colony.

The other alternative, accepting the budding end of the stolon as the organization centre, does not seem probable. During the budding process every zooid would be produced in the terminal end of the stolon and an analysis of relations in the terminal portions of the growing graptolite branches indicates that budding started from the actually terminal zooid of a colony (comp. fig. 8 B) which, in turn, would produce the next zooid. Analogies with the living pterobranchians (*Cephalodiscus*) suggest that budding occurs within a definite zone at the base of the mother zooid. Hence, should the successive terminal zooids be regarded as the inducing centres affecting the descendant zooids budding from them, we could conclude that the intensity of this induction and at the same time the extent of physiological isolation would be very much the same in all the zooids of one colony. Similarly, relations in *Rhabdopleura* (comp. fig. 8 A) indicate that buds are produced at a definite distance from the terminal (leading) zooid, at the base of its contracting peduncle. The growth of the stolon here is realized through the intermediary of the permanent immature, terminal bud, whereby this development type differs from relations common in graptolites (Kozłowski, 1948)¹². This, however, clearly shows that in any case the variability of thecal shape cannot be explained by the

¹² Fundamentally the same relations as in Graptoloidea have been also ascertained in Dendroidea (Kozłowski, 1948) where the growth of branches occurs by mediation of stolothecae which are merely the proximal immature portions of autothecae. The individuals contained in them may be regarded as the terminal immature autozooids.

supposition that the actually budding portion of the colony might have been the inducing centre.

On the other hand, the recognition that the terminal budding end of the stolon had progressively decreased activity and caused correspondingly diminishing induction in successively budding thecae, would lead on to the conclusion that the diminishing activity may merely be an expression of its concealed senescence. This hypothesis, however, has no sound base since following it we would have to accept weaker activity of distal thecae as compared with the proximal ones, due to the origin of the former from tissues of the senescent end of the stolon. This is, however, contradicted by evidence showing that the distal thecae attain the greatest dimensions and often produce the most complex apertural apparatus (e. g. in *Cucullograptinae*). This requires additional supplies of the peridermal substance and suggests their high morphogenetic and physiological activity (comp. p. 156—157)¹³.

Doubtlessly, the growing budding terminal end of the colony (terminal distal zooid) must have been the centre of intense physiological activity (formation of new tissues, histogeny). In a certain sense we might also speak of the occurrence in graptolite colonies of a "double gradient" (Huxley & de Beer, 1934), similarly as in annelids and arthropods. Two fundamentally different processes are here manifested suggesting two independent centres of strongest activity. One of these consists in the formation of new tissues (distal terminal zooid in graptolite colonies, the subterminal growth zone in annelids and arthropods); the other is a process of the induction and control of morphogenetic processes, associated with corresponding specialization of tissues (probably the siculozooid in graptolite colonies, the head in annelids and arthropods), (comp. also Bulman, 1951, 1958).

The activity of the first factor displays rather rapid decrease from the distal to the proximal end, as is indicated e. g. by a series of terminal thecae of *Lobograptus scanicus parascanicus* (Kühne), (comp. fig. 8 B). The activity of the other factor gently decreases in the distal direction. Colonies without sicular region (comp. p. 162) indicate even that the sicular centre, playing an important role in astogenetic development, is by no means necessary for mere budding and life of the colony.

According to the now accepted views, the action of the sicular centre is comparable with that of the inductor, while the reaction of

¹³ Certain structural changes in terminal autothecae of dendroids: abbreviation, bending, may however be explained as senile modifications in terminal branches (Kozłowski, 1948, p. 28—29). Within terminal autothecae their manifestation sometimes regularly increases. These processes do not, however, to any considerable extent affect thecal morphology. In Graptoloidea moreover distal thecae are on the whole longer than the proximal.

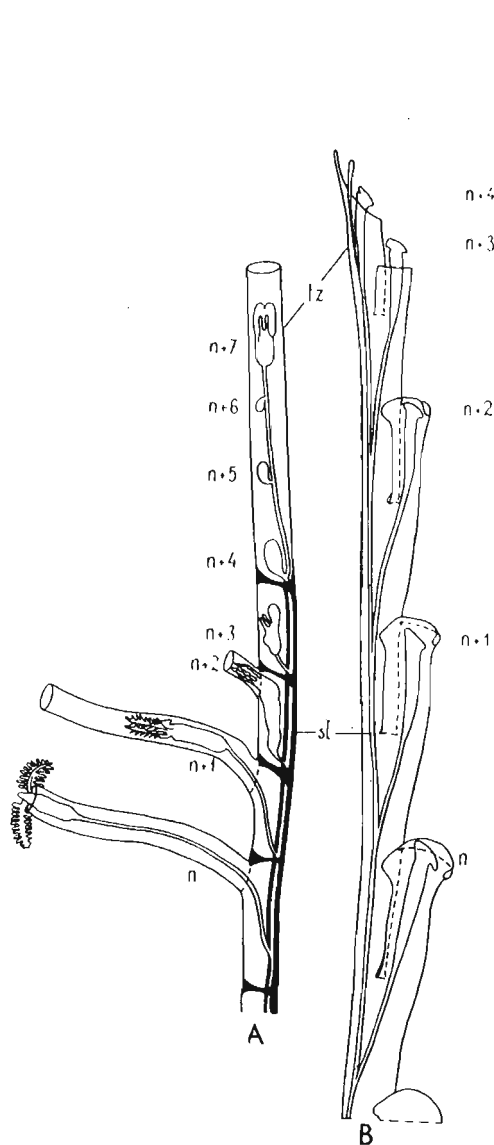


Fig. 8.— Comparison of terminal, growing tips of a colony: A in *Rhabdopleura* (after Lankester, from Grasse, 1948, and after Bulman, 1955; combined), B in *Lobograptus scanicus parascanicus* (Kühne), partly reconstructed from two combined fragments (boulder S. 137, S. 181); *st* stolon, *tz* terminal zooid, *n-n+7* successive zooids.

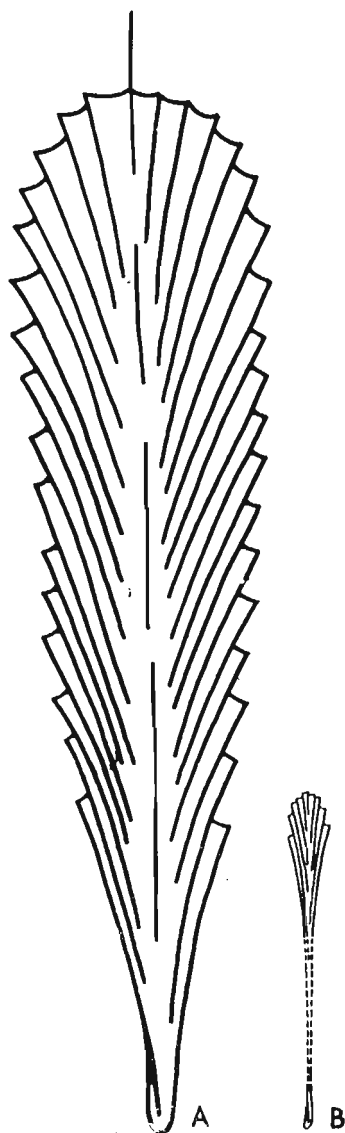


Fig. 9. — Interrelation of changes in shape and size of thecae and in shape and size of rhabdosome in Petalograptinae: A *Petalograptus folium* (Hisinger), reverse side; B *Cephalograptus cometa* (Geinitz), reverse side. In both specimens length of 1^d is shown with equal length (based on Bulman, 1955, fig. 63, 6b and 7b).

the blastozooid tissues to the inducing factor may be compared with the phenomenon of "competence" or "Reaktionsfähigkeit", observable in the developmental physiology (Waddington, 1940, Needham, 1942).

The physiological dominance of the sicula in relation to the remaining thecae of the rhabdosome must have been most likely caused by the spreading along the rhabdosome axis of certain active morphogenetic substances, probably produced by the tissues of the siculozoid. In their biological properties these substances must have resembled animal hormones and plant growth substances (auxins). Close analogies surely existed between these factors and certain morphogenetic substances produced by "organizers" in embryonal development of animals and responsible for the phenomena of embryonal induction. Ample literature references on this problem are given in papers by Waddington (1940), Needham (1942), Lehman (1945), Barth (1949) and Wagner & Mitchell (1955). Such substances seem likewise responsible for definite growth relations (Huxley, 1932, 1942). Huxley indeed postulates that this is due to the "partition of some substance responsible for growth potential" (1950). When the successive thecae differ in allometric changes, it could be accepted that the substance produced by the siculozoid might control the mode of growth and the growth relations in the particular organs of each successive zooid, their "secretory behaviour", hence thecal shape too.

Astogenetic succession in graptolites where it is restricted to "growth gradients" may be illustrated on certain pristiograptids, e. g. *Pristiograptus dubius* (Suess), (comp. fig. 2 F). Thecal modifications here are expressed by certain allometric changes. In Petalograptinae the relations are somewhat more complex (comp. fig. 9 A, B). *Cephalograptus* Hopkinson, belonging here, is distinguished from *Petalograptus* Suess in greater elongation of thecae reflected in the shape of the whole rhabdosome. Perfectly reliable data regarding the mutual phylogenetic relation of these forms are not available. However, it is known (Bulman, 1955) that *Petalograptus* appeared earlier, while intermediary forms occur, linking these extreme morphological forms. The nature of the changes here is readily understandable on bringing these forms to the same length dimension of $th\ 1^1$, whereby the effects resulting from proportion changes are very much stressed (fig. 9). The presence in these graptolites of a distinct growth gradient permits to regard their colonies as an integrated unit under a common physiological control.

In many graptolites astogenetic changes are not confined to such simple changes concerning the size and proportions of thecae. The here given examples (fig. 1 A, 2 A—C) illustrate relations occurring

when the progressive thecal modifications attain the "qualitative stage" (presence or absence of certain structures, or their deeper changes). It should be concluded that on the whole such substances might have altered the degree of the phenotypic manifestation of genetic factors in particular individuals. The degree of the modifying effect must have been controlled by the amount of the given substances morphogenetically active in tissues of the various zooids.

Certain structural characters of thecae are better stressed either proximally (group A, 2 a) or distally (group A, 2 b), (p. 134, 137). Hence it reasonably follows that in relation to definite characters or groups of characters these substances acted respectively as stimulators (group A, 2 a), or as inhibitors (group A, 2 b). In the former case, when the substance produced by the siculozoid has a stimulating effect, certain characters were phenotypically more strongly manifested in the proximal portion of the rhabdosome, owing to the highest concentration (amount) of these substances. In the latter case, when the substance produced by the siculozoid behaves like an inhibitor, features whose phenotypical manifestation it affects, would be strongest in the distal region of the rhabdosome where the concentration (amount) of these substances is lowest. In both cases, however, *the regular decrease of the amount of morphogenetically active substances, modifying the phenotypic manifestation of characters, would be responsible for the occurrence of a definite morphological succession of thecae.*

Causes of the regular decrease in the concentration of morphogenetic substances along the colonial axis may be of different nature. The decisive factor here may be the mode of distribution of these substances from one local centre producing them (siculozoid). Accepting constant activity of the inducing centre, properties of the particular zooids would be determined by their distance from that centre, growing progressively with astogeny, i. e. by increased physiological isolation. The mechanism of the distribution of morphogenetic substances might suggest certain analogies with the process of diffusion thus explaining the formation at a certain moment of a regular concentration gradient. On the other hand, however, the spreading of such substances as the auxins is a process totally differing from that of diffusion. The transport of these substances ought to have displayed some polarity too, resulting in a direction opposite to the action of gravity forces. The available physiological data (Went & Thimann, 1937, 1945) apparently contradict that gravitation can actually be an agent determining the biological polarity. Hence the concentration of active substances in the proximal end of the colony (physiologically lower part of a colony) cannot be

regarded as a mechanical effect of the orientation of colonial axis. The spreading of the active substance along the rhabdosome axis was undoubtedly connected with the definite mode of its transport, and the growing terminal zooid of the stolon must have been here a certain "point of attraction". Nevertheless it would hardly be possible to account for the constantly diminishing concentration of active substances by the concentration gradient alone, since it could lead to gradual equation of differences. Hence, we might perhaps as well agree with Waddington's (1956) opinion that the regularly decreasing concentration of morphogenetic substances is referable to the progressive exhaustion of definite substances, necessary for the budding and growth of the successive individuals of a colony. These substances, produced in the tissues of the oozoid and transported along the rhabdosome would be partly exhausted in the budding process, while the induction would be in each case realized by the still available amount of substance. This would diminish regularly with the development of the colony (comp. p. 148). Physiologically the mechanism of this process would remind us of the gradual "dilution" of pigment among the progeny of the flour moth *Ephestia*, in the case of the absence in the genotype of gene *A* which is necessary for the production of pigment. Individuals *aa* bred from the crossing of the female *Aa*, and the male *aa* dispose of a certain amount of pigment supplied by the egg cell. Owing to lack of ability for pigment production, it is dissolved during the process of cleavage and differentiation of tissues. In result, the individuals grow paler, while in the following generation the effect disappears (Kühn, Caspari & Plagge, 1935; Plagge, 1939). In graptolites the morphogenetic substance behaves similarly. "Introduced" into the colony by an oozoid capable of producing it, this substance would during blastogeny likewise become dissolved and exhausted. This would lead to its regular gradient. The fact that the substance would supposedly be produced by the oozoid only, is physiologically understandable since it is the oozoid alone which owes its origin to a sexual process and which is probably subject to a complex metamorphosis (Kozłowski, 1948), while the budding of the remaining members of a colony corresponds to simple blastogeny.

The causes of astogenetic variability may be also looked for in the gradual senescence of the colony, manifested by the regularly diminishing reaction ability of tissues, i.e. their ability for phenotypic manifestation of definite genetic factors and for differentiation. This is contradicted, however, by such facts as the stronger manifestation of certain morphological characters in the distal portion of graptolite colonies, as compared with the proximal portion and, generally speaking,

by their being "introduced distally" in many phylogenetic graptolite lineages. This does not at all mean that, with colonial growth, the successive zooids gradually lose their ability for phenotypic manifestation of the respective genetic factors and for differentiation (comp. p. 152). Much more likely are the first two hypotheses claiming lack of any notable differences in the reactiveness of the successive zooids. The reactiveness potential of the colony must have undergone changes "in toto" according to a similar pattern for the whole colony.

Independently, however, of the mechanism of this process, it must have resulted in the progressive and regular decrease of the amounts of definite substances available to the successively budding zooids. The most sound and mutually complimentary hypotheses are those postulating that the sicular portion was the centre producing morphogenetically active substances, and that subsequently these substances were successively exhausted in the budding process of the individual zooids of a colony. Hence in further considerations, we assume to be dealing here with a decreased concentration, connected with the distribution gradient of the given substances from the proximal part. The supposition for the regular decrease of concentration of the substance, produced by the siculozooid, is based on analogous phenomena in the distribution of growth hormones in plant stems. These likewise display a more or less regular decrease of concentration, associated with a constant direction of their transport (Went & Thimann, 1937, 1945). Similar relations occur in many animals. E. g. a regular gradient of the regeneration rate has been ascertained in *Tubularia* (Barth, 1938, 1940). Particularly interesting are the investigations of Gast and Godlewski (1903) who have demonstrated in the colonial hydrozoan *Pannaria cavolinii* the existence of a regular regeneration ability gradient, manifested along the axis as well as on the secondary branches of the colony. The transport of morphogenetic substances has likewise been ascertained in many animals, but its mechanism is not very well known. In *Drosophila* the hormonal substances are transported by means of the lymph (Ephrussi, 1942), while in *Ephestia* streams of such substances and their probable course have been ascertained by Kühn and Henke (1936). Students of these and similar problems have even created such convenient terms as "pigment-stream" or "determination-stream" to emphasize the process of the distribution of the corresponding morphogenetic substances (Goldschmidt, 1938). In graptolite colonies the spreading of such substances might in the first place be effected through the stolon, possibly also the extrathecal membrane connecting all individuals of a colony.

Organization of multiaxiate colonies

The nature of the fossil material does not naturally permit experimental verification of the correctness of the just stated views. The palaeontologist, however, is not quite helpless in this respect since he is in a position to examine phenomena deserving to be called the experiments of nature. Among them we may include the development of graptolites with secondarily branched colonies which have probably evolved from forms originally provided with one branch only (*Cyrtograptus* Carruthers, *Diversograptus* Manck, *Linograptus* Frech). Out of these forms, *Cyrtograptus* alone (fig. 10) has been studied more thoroughly. Its cladogeny, i. e. the mode of secondary branching has been recently described by Thorsteinsson (1955). On this form we can check up the supposed dependence of the distance of given theca from the sicula and its shape. In the species studied by Thorsteinsson (*C. rigidus* var.) the thecae of the main stipe display normal morphological succession. In the proximal part they are more strongly bent and provided with longer apertural spines than distally. Similar relations likewise prevail in some other structural features of thecae. Thus thecal succession on the main stipe of the rhabdosome fits into graptolite type A, 2a — biform — (comp. p. 137), thecal shape being determined conformably with the stated above hypothesis on its distance from the original zooid. However, the shape of the first formed cladial thecae no longer agrees with this pattern. In shape the first cladial theca does not correspond to that in the first theca of the main stipe placed immediately behind the mother theca of the cladium, but it corresponds with much more distal thecae, hence being in a certain sense „retarded”. We are dealing here with two distinct phenomena. 1) According to Thorsteinsson (1955) and Bulman (1955, 1958) the formation of the cladium is somewhat delayed. Before the first signs of growth of the first cladial theca, some 3—4 next thecae have appeared on the main stipe, and another 3—4 will have been added before the first cladial theca is completed. 2) Moreover the first theca of the cladium corresponds closely in shape with that of the theca simultaneously being produced on the main stipe though the latter is much more remote from the sicula than the former. Further thecal development on the main stipe and on the cladium is parallel and occurs at the same rate. In figure 10 thecae joint by broken lines are those occurring on different branches of the rhabdosome, but budding very nearly simultaneously and closely resembling one another. Hence it may be supposed that it is not the distance from the original zooid, i. e. thecal position that determines

the shape of thecae in *Cyrtograptus* colonies, but the age of the colony as a whole, i. e. the time of budding (fig. 10).

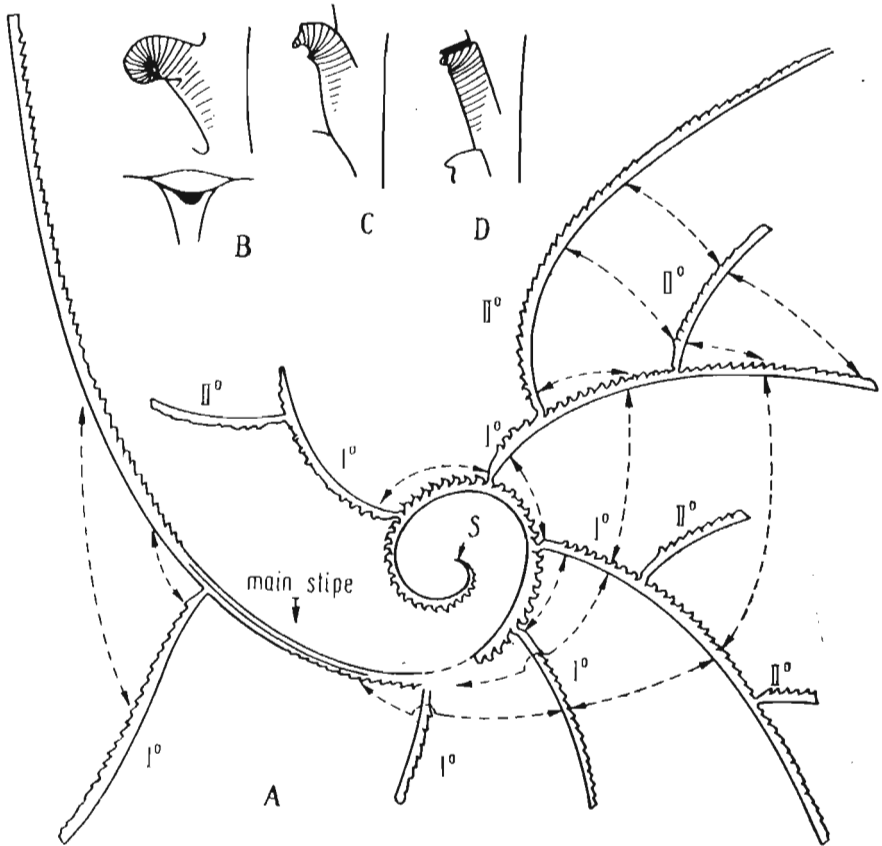


Fig. 10. — Diagram showing structure of a complex colony in *Cyrtograptus* Carruthers. Approximately contemporaneous thecae are connected by broken lines (A); B-D shape of proximal, medial and distal thecae shown diagrammatically; S sicula, I° lateral branches (cladia) of first order, II° lateral branches of second order; point where twisting of rhabdosome axis occurs indicated by arrow (from Bulman, 1958; redrawn with some modifications).

In order to explain the first of the here mentioned phenomena, i. e. that of delayed production of cladial theca, it should be noted that in *Cyrtograptus* the budding of the cladium originates indirectly through the tubular outgrowth of the aperture of one of the thecae in the main stipe. The tubular prolongation formed by it is the beginning of the first cladial theca. These facts probably indicate that the cladium is not produced by the stolon, but by way of budding from one of the thecae on the main stipe. This sheds some light on the factors supposedly responsible for the "retarded" cladial budding

as compared with that on the main stipe. They may be the biological analogues of relations observable on the main stem and axillary shoots of plants. We are here dealing with a sort of dominance of the main stem over the axillary shoots (apical dominance; Child, 1915; Snow, 1925, 1929; Thimann & Skoog, 1933, 1934, *vide* Went & Thimann, 1937, 1945)¹⁴.

The inhibition of the growth of axillary shoots by the main stem may be removed by the inhibition of the activity of the centre of dominance which is known to be in the growing tip. According to Thimann (1937) this inhibition process may be the direct result of the influence of auxins produced by the growing tip of the main stem, also partly of the diminished supply of food substances. In the writer's opinion this sheds some light on the mode of cladial generation in *Cyrtograptus*. The here noted phenomenon of retarded development of the cladium as compared with that of the main stipe was most likely due to a sort of biological inhibition referable to the dominance of the main stipe over those of the cladium.

The background of the dominance may be found in the fact that the cladium which buds through the intermediary of the mother zooid has been supplied with a smaller amount of the active substances, perhaps of the nutritive too, than thecae on the main stipe which are directly interconnected by the stolon. The phenomenon that the first cladial theca corresponds morphologically to the simultaneously produced thecae on the main stipe — in spite of being much nearer to the siculozooid — is readily explained by the inhibition of the development of the lateral branches. To a certain extent the cladium may be regarded as the lateral branch of a colony. In many plants (peas, beans) the simultaneous growth of two shoots is possible only when they grow at about the same rate and have the same physiological activity. Otherwise the growth of one of the shoots will be inhibited. Analogously, in graptolite colonies, the morphogenetic activity of the first cladial theca must have attained an equal level as that of the just then budding theca of the main stipe. In the first place the two zooids must have had at their disposal equal amounts of morphogenetic substances. These were correspondingly smaller than that controlling thecal growth of

¹⁴ Close analogies have been ascertained in many colonial hydroids (e.g. Child, 1941, p. 319) since, however, the physiological mechanism of dominance in these forms has not been thoroughly investigated, the use of plant analogies is here found to be more convenient. The experiments of Gast and Godlewski (1903) on the regeneration in the colonial hydroid *Pennaria cavolinii* of axial fragments provided with a cladium shows that the cladium may be subject to degeneration and a sort of resorption, while the tissue material of the cladium is used up for the growth of the axial portion. This suggested the distinct physiological dominance of the axial portion over the lateral branch.

the main stipe situated at the same distance from the sicula as the first cladial theca. With stabilized level of the reaction ability of tissues, the reduced amount of hormones would act analogously as the appropriately increased distance from the siculozoid. The morphological analogies of the first cladial theca with that in the simultaneously produced thecae of the main stipe apparently suggest that at the time of budding the concentration of the morphogenetically active substances was nearly the same in the ends of both branches. Hence the production of the bud for the cladium would probably be connected with the attainment of a certain equilibrium of the concentration of substances in the main and lateral branches. We have here an analogy with relations in the growth of axillary shoots in plants and colonial animals and the attainment of a certain equilibrium between the activity of growing tips displaying simultaneous growth (e. g. in plants, Child 1915, et alii; in animals similar relations e.g. in Tubularia; Child & Watanabe, in Child, 1941). This concept correlates the asto- and cladogeny in *Cyrtograptus* with those in other monograptids, suggesting that similar shape of simultaneously budding thecae was caused by equal amount of morphogenetic substances available for these zooids.

For the particular species of cyrtograpti, provided with several lateral branches (comp. fig. 10), their mutual spacing is a characteristic feature (Bouček, 1933; Bulman after Thorsteinsson, 1958). In *C. radians* Törnquist, a cladium is produced by every successive theca, in *C. mancki* Bouček — by every second one, in *C. ramosus* Bouček — by every third or fifth one¹⁵. The distance of the first branch from the sicula is a constant specific character too. Spacing of the lateral branches of the rhabdosome, closer in some species, more distant in others, seems to be a genetically controlled feature. Hence it seems reasonably sound to claim that every lateral branch is so to say a centre of dominance of secondary order affecting some part of the main stipe too. This would be an analogy with the "correlation chains" occurring in the embryonal development of animals, whose links are the successive organizers of decreasing orders (Šmalgauzen, 1938, *vide* 1946). It has been similarly ascertained that the axillary buds of plants, though themselves controlled by the main centre of physiological dominance, in turn exercise a dominance over the main stem preventing the formation of new axillary buds over a certain area (Child, 1915, 1941). Relations similar to those between the main stipe and the lateral branch of first order would occur between lateral branches of the first and

¹⁵ According to Bouček (1933) in *C. ramosus* the distance between lateral branches regularly increases distally.

secondary order in cyrtograpti provided with them. The complete *Cyrtograptus* colony, with a complex organization pattern, would then present an intricate system, self-regulating by way of complicated physiological gradients.

Somewhat different relations must have occurred in forms where several independent centribranchiate stipes radiated from the sicula or the sicular region. To such forms are referable many representatives from the groups of Dichograptidae and Leptograptidae. Out of the monograptids, *Linograptus* Frech (Jaeger, 1959) and also to a certain extent *Diversograptus* Manck, may be referred to such forms. The latter is by many authors claimed to be a graptolite provided with two stipes independently radiating from the sicula (Manck, 1923; Bouček, 1933; Bulman, 1938; Strachan, 1952; Bulman, 1955). Other authors, however (Bouček & Přibyl, 1953; partly Jaeger, 1959), question this standpoint. In these genera the thecae are straight, not distinctly differentiated (*Linograptus*), or again hooked, nearly homogeneous over the complete length of each cladium (e.g. the typical *Diversograptus* described by Strachan, 1952). They do not throw any new light on the here considered problem. In more thoroughly investigated Dichograptidae thecal succession on every branch is uniform, as if the colony consisted of an assemblage of independent rhabdosomes, linked by the sicular region where bifurcation occurred.

A phenomenon recently stressed by Jaeger (1959 in litt.) seems to be more interesting. It ascertains the occurrence of monograptid forms provided with a region of divergence from which divergence of thecae occurs in two opposite directions. This region, however, is not here the sicular region. The thecae and their succession are uniform in both directions. In this form, which might only provisionally be named "*Diversograptus*", the thecae do not show the astogenetic variation, being virtually analogous in size and shape, and suggesting the lack of polarity caused by absence of sicula.

Similar cases of the divergence of rhabdosomes have been noted by the present writer, among others in *Lobograptus scanicus parascanicus* (Kühne). The divergence of rhabdosomes there are distinctly connected with the preceding damage, breaking off of a part of the colony¹⁶.

Of some interest is the occurrence in graptolites of rejuvenation among colonies of *Dictyonema flabelliforme* (Eichw.), (Bulman, 1950), taking place during regeneration of damaged fragments of a colony. Rejuvenation is marked there by change of branching frequency ap-

¹⁶ Such cases show evidently that the presence of sicula is not necessary for the life of a colony and budding process, being however the factor determining the course of normal astogeny (comp. p. 152).

proximating to that at the proximal end of rhabdosome. Such cases are to a certain extent out of the rule of gradients controlling the graptolite colonies. However, similar phenomena are observable during regeneration of many living organisms where cut and wounded tissues disturb existing physiological patterns causing the formation of new gradients (comp. Child, 1941). One may expect here the mobilization of the amounts of active substance that have still persisted, possibly even a secondary stimulation of tissues to secretion and origin of a new gradient in spite of the old one.

*Changes in shape and in the mode of development
of the rhabdosome*

While changes in thecal structure during astogeny may be readily accounted for by the morphophysiological gradient theory, those concerning the rhabdosome shape do not seem very easy to explain. In *Dendroidea* the shape of the colony is fairly distinctly defined by the number of branches, their mode of branching and of connection of one to another. In higher *Graptoloidea* the colony grows along the thin peridermal thread representing the *virgula*. According to Kozłowski (1948) the nema is formed inside a tubule built up of the soft extrathecal tissue membrane and coating the nema in the same way as the insulator envelops the electric wiring. This suggests the action of some factors whose biological effects resemble those determining the mode and direction of growth in plant shoots which we know to be controlled by the distribution of auxins (Overbeek, 1938; Shafer, 1939). Changes in the distribution of auxins have a bearing on the growth direction of shoots. Similarly, curvatures of the nema or the *virgula* might occur owing to changes in the distribution of morphogenetic substances in the growing tubule of soft tissues coating the nema and in turn influence the shape of the rhabdosome. Similar factors may influence the growth direction of branches by affecting the position of the stolon and thus determining the mode of growth of branches as pendent, scandent or intermediary.

Suggested physiological mechanism of changes in the growth direction of rhabdosome needs, for causal explanation of evolution, the support of some selective factor. According to Elles (1922) a rather general tendency of numerous graptoloids trends toward attainment of a scandent direction of growth is to be seen in the protection of the nema "which is so vitally necessary in the life history of the organism. Thus whilst in the earlier pendent graptolites this structure is left

completely unprotected, the scandent forms even if uniserial protect it better" (p. 175). Bulman (1933), however, stressed that "although if it is regarded as an example of Darwinian selection, it must be admitted that the attainment of the end was a remarkably slow process, conferring little advantage in its early stages, during which forms with an unprotected nema survived with considerable success" (p. 316). The selective advantage in changes of growth direction of rhabdosome is, however, to be seen also, as it has been shown by Lapworth, in feeding-mechanism, probably more effective for animals provided with lophophore apparatus, directed toward the upper surface of the sea, and constituting a kind of a screen directed toward the source of nutritive particles. This may be a factor stimulating any, even small change in direction to erection of stipes.

The mode of astogenetic development is an important morphological feature (Elles, 1922; later fully elaborated by Bulman, 1938, 1955). On the whole, the various types of colonial development are determined by: 1) mode of thecal budding — the number of alternating thecae and of crossing canals being generally increased during the evolution of graptolites; 2) growth direction of thecae and of branches — the progressive upwards growth being the general trend. In some trends gradual modifications in the mode of astogeny have been ascertained (Davies, 1928; Waern, 1948).

In respect of the mode of budding some graptolites may be regarded as "biform". They represent a "mixed condition" — proximal thecae alternate in origin, distal thecae are separated by median septum, forming two independent series. "Non-septate" graptolites, with alternate type of budding throughout the rhabdosome may be regarded as "uniform" in respect of the mode of budding. These data suggest the possibility of manifestation of a certain sort of polarity responsible for differences in the budding of proximal thecae as compared with the more distal ones. The factor responsible for the alternating type of development would, in augmenting its effectiveness, increase the number of individuals displaying the alternating mode of budding. We might surely expect here the occurrence of a gradient associated with a kind of "threshold effect". The decrease of the activity of a given factor below a certain threshold value would bring about, conformably to the "all or none" reaction, a rather abrupt passage from the alternating to the biserial type of development (comp. p. 185). The development of the rhabdosome seems to be also an expression of gradients governing the organization of graptolite colonies.

The reduction of the number of individuals in graptolite colonies

is an interesting phenomenon of their evolution. In Bulman's opinion (1939, 1955) this is the general tendency in graptolite evolution. The number of individuals is supposedly the greatest in colonies of *Dendroidea*, the smallest in those of Upper Silurian Graptoloidea (*Monograptidae*). Urbanek (1958) has stressed that this seems applicable to the Lower Ludlovian forms examined by him with rhabdosomes shorter than those in the supposedly related Wenlockian forms. Jaeger (1959), however, has pointed out that forms with extremely long rhabdosomes occur in the Upper Ludlovian besides those with moderately short ones. Quite apart from the possible general tendency for a reduction of colonies in all graptolite trends this is particularly striking, however, in some trends. The family *Corynoididae* is a good example of this reduction, its representatives having a rhabdosome consisting of the sicula and 1—3 thecae only. The genus *Nanograptus* Hadding displays strongly reduced colonies too.

It is interesting to note the relative increase of the size of the sicula accompanying the reduced number of individuals. In *Corynites* Kozl. it attains 4.0—4.5 mm, in *Nanograptus* 2.5—3.0 mm¹⁷.

Progressive structural modifications associated with the simultaneous reduction of the colonies sometimes occur also in the sicula which develops a complex apertural apparatus (Kozłowski, 1953, 1956, in *Corynites*). Cases of this kind, by Kozłowski called "colonial neoteny", suggest that colonial growth has been here to some extent replaced by the growth and differentiation of its first individual, i.e. the siculozoid. The colonial organizer of the colony would at the same time become the reacting centre which might have had some bearing on the reduction of the colony. The physiological mechanism of these phenomena may to some extent resemble hereditary dwarfism in plants (Overbeek, 1935, 1938) being an effect of the presence of some enzymes decomposing growth substances and causing strong decrease of their amount in tissues. The considerable use of similar substances by the growing siculozoid in graptolite colonies may have an analogous influence on the size of the whole colony.

The reduction of the periderm occurring in some graptolite trends likewise agrees with the general laws governing the gradients. A vestigial membraneous periderm persists in the proximal thecae of many graptolites. In the next thecae this becomes discontinuous and finally disappears completely (particularly so in *Retiograptus* Hall and

¹⁷ In primitive Graptoloidea the length of the sicula ranges usually from 1-2 mm. Only exceptionally it is below this figure (0.8 mm), occasionally being up to 3-4 mm, while the maximum length of siculae in Graptoloidea is 5 mm.

to some extent in *Orthoretiolites* Whittington, and *Pipigraptus* Whittington. These forms may be to some extent termed "biform" in respect to the presence and absence of periderm in thecae of the same rhabdosome. In *Archiretiolites* Eisenack the sicula only is provided with the periderm, while the remaining thecae have clathria only. In other forms the periderm becomes completely reduced throughout the rhabdosome length ("uniform" in respect to absence of periderm). We are here dealing with a gradual loss of the ability to produce periderm, the factor controlling this ability persisting longest within the proximal portion. This is an excellent analogy with the picture given by thecal succession in many graptolites (reduction of periderm is a "character introduced distally"), and must have been caused by similar factors.

From our considerations it follows that graptolite colonies are characterized by a definite astogenetic succession of thecae hence also by probable differentiation of individuals of a colony; they may, therefore, be interpreted as units integrated by the dominant influence of the sicular centre. Dominance would be realized through the spreading of active substances probably produced by the siculozoid, in nature very much like the hormones. The extent of modification of the particular zooids would be correspondingly determined by the degree of concentration of these substances displaying its gradient along the rhabdosome axis.

IV. GENETIC ASPECTS OF THE ORGANIZATION OF GRAPTOLITE COLONIES

Supposed genetic nature of graptolite colonies

The supposed genetic mechanism in the evolution of graptolite colonies may be deduced from 1) the basic biological properties of graptolite colonies, 2) the basic laws of genetics. Modern views (Kozłowski, 1948) claim that a graptolite colony is represented by 1) the oozoid which is metamorphosed into the siculozoid, and 2) the remaining zooids, corresponding to blastozooids, i.e. produced in an agamic pattern by way of budding from the siculozoid. Considering that a graptolite colony owes its origin to agamic reproduction (budding) from a single zooid, the founder of the colony (siculozoid), it may be referred to as the "clone". Hence, genetically speaking, a graptolite colony is an assemblage of zooids all displaying the same genotype, that of the oozoid. This fact bears important genetic consequences. Namely, *individual variability in graptolite colonies may only express the varying phenotypic manifestation of genetic factors, characterizing all the*

individuals of a colony, but cannot represent genotypic differences among the particular individuals of a colony; occurrence of somatic mutation in blastozooids as changes manifested by abrupt irregularity of thecal succession, is here neglected. Especially the regular morphologic succession of characters in biform graptolite colonies could only be an expression of the various degree of phenotypic manifestation of genes belonging to a genome common to all the zooids of a colony.

Our earlier considerations have led to the conclusion that this phenotypic effect would be controlled by the amount of certain substances produced probably by the siculozooid and distributed along the colonial axis. Hence this substance would supposedly have the properties of a "gene controlled substance", i.e. it would be connected with the presence of genes acting as stimulators or inhibitors of some other genes (modifying genes). The action of these genes may be realized by the production of substances with properties like those of hormones. The view that genes are responsible for the production of enzymes, inhibitors or hormonal substances of varying morphogenetic effect, is an orthodox concept in genetics (Goldschmidt, 1938, and earlier; Waddington, 1940; Needham, 1942; Wagner & Mitchell, 1955). These facts are widely known in genetics, beginning with the classical experiments of Sturtevant (1920) on the inhibition of manifestation of mutation "vermillion" (changing the eye colour) in the gynandromorph of *Drosophila* under the influence of an ovary-produced substance, through thematically similar studies of Beadle and Ephrussi (compiled in Ephrussi, 1942), of Kühn, Caspari & Plagge, 1935, et alii (compiled in Plagge, 1939) on factors controlling the pigmentation in *Ephestia*, and many others (comp. with the more comprehensive discussion in Waddington, 1940, Needham, 1942). Hence it seems justifiable to admit that in graptolite colonies a hormone-like, diffusible substance was the factor modifying the manifestation of hereditary characters.

The recognition that, in some cases, the morphogenetic substances spreading along the rhabdosome acted as stimulators and in others as inhibitors of the manifestation of certain alleles, coincides with data from the field of physiology and genetics. Indeed, it is often ascertained that even the same substance, depending on its concentration, may either act as a stimulator or as an inhibitor of certain processes (e.g. auxins in plants; Thimann, 1937). Moreover, modern genetics claim that the phenotypic manifestation of a given allele is controlled by a number of genes and depends on a whole genome. Hence it may be expected that within various phylogenetic trends various factors controlled the mutual relations of alleles and of their modifiers, the latter acting either as stimulators or as inhibitors.

Waddington's views (1940, p. 62—65) suggest that the substance produced by the tissues of the sculozoid would be classified as a "localized gene effect". The morphogenetic substance produced by definite tissues or organs would subsequently be "diffusely localized" or transported by "blood stream", body fluid, and permeate the whole system ("permeating"). Analogous relations as those here accepted for graptolites have likewise been ascertained among insects *Drosophila* and *Habrobracon*.

Moreover genetics have at their disposal a number of facts indicating considerable morphogenetic effects due to genetic changes which influenced the amount and distribution of such substances. In plants the general habitus is determined by the amount of produced auxins. This may be controlled genetically and cause e.g. dwarfism of plants (Overbeek, 1935, 1938). Similarly, the distribution of auxins may be subject to changes owing to mutations, resulting in the formation of "lazy" varieties of maize (Shafer, 1939, Overbeek, 1938). Detailed discussion on the physiological significance of the growth and morphogenetic substances in plants is contained in works by Bünning (1953) and Tukey (1958). In view of the equally strong effect of substances on animal organisms (organizers, sex hormones etc.) there seems to be little doubt that such factors could also control the manifestation of some genetic factors in graptolite colonies.

The astogenetic variability of a definite morphological character in a graptolite colony would, therefore, express differences in the phenotypic manifestation of the same genetic factor or factors. It would follow that these mutations had a particularly broad range of manifestation controlled by environmental changes (amount of hormones!). Similar facts, however, concerning the varying degree and intensity of manifestation of definite substances, depending on environmental condition of "reaction", have been thoroughly studied in a number of cases. Particularly adequate knowledge has been obtained concerning the effect of temperature (Harnly, 1936 *a, b*) on the shape and size of wings in the vestigial and pennant mutants of *Drosophila*, also on the temperature controlled number of eye facets of the *bar* and *ultrabar* mutants of *Drosophila* (Hersh, 1930, *vide* Goldschmidt, 1938; also comp. the discussion on "termophenes" in Needham, 1942, and Wagner & Mitchel, 1955). In *Bonellia*, the larvae are subject to powerful morphological modifications; under the influence of the hormone produced by female proboscis they alter into dwarfed males. The degree of modification is controlled by the amount of the absorbed hormone, its concentration and the time which they spent on the proboscis (Baltzer, 1925, 1937, *vide* Hartmann, 1943). This fact illustrating the

phenotypic sex determination proves beyond doubt that zooids of graptolites too may have undergone powerful changes under the influence of similar hormonal factors.

The supposed evolutionary mechanism in graptolite colonies may, therefore, consist in genetic changes (mutations) affecting the activity of modifying genes, responsible for production of stimulating or inhibiting substances, or in successive formation of a series of mutations correspondingly altering the morphogenetic properties of blastozooïd tissues. Changes in the activity of genetic modifiers, e.g. decrease of inhibition, would be expressed by stronger phenotypic manifestation of characters in some members of the colony and by their manifestation in an increased number of zooids. Thus, the expressivity of a definite gene, and, moreover, its penetrance, would be changed in a population formed by a colony. Given the constant activity of modifiers the same effect will result from changed activity of major genes responsible for changes in the phenotypic manifestation ability of tissues. E.g. a mutation series of a gene or genes forming a series of changes characterized by increasing phenotypic manifestation ability of tissues, will result in approximately similar morphological effects as a mutation series of inhibiting modifiers, characterized by successively decreasing activity in production of inhibiting substance. Both these factors might have a decisive bearing on the mechanism of gradual changes of colonial organization.

Evolutionary changes in graptolite colonies are, therefore, expressed in two ways: 1) by changes of the degree of manifestation of definite characters in the particular zooids of a colony and, at the same time, by 2) changes in the number of individuals in which a definite character is on the whole phenotypically expressed. Since all individuals are genotypically identical, these differences are a consequence of changes in the phenotypical manifestation of same factors. Hence, the evolution of graptolite colonies is conveniently described by using the terms "*expressivity*" and "*penetrance*". They have been introduced into genetics by Timoféeff-Ressovsky (1931 and earlier) and excellently characterize the various effectiveness of the phenotypic manifestation of genetic factors¹⁸. The process of spreading or progression of a new character (thecal form) along the rhabdosome (comp. p. 139) so many times described from evolutionary graptolite series, would, genetically speaking, merely be an expression of increasing *penetrance* of cor-

¹⁸ After Needham (1942) these terms might be defined as follows: "*penetrance* — the percentage of animals carrying the genes which manifests its effects (percentage of phenotypic effect); *expressivity* — the extent to which an animal carrying a gene and showing it is affected by it (the relative severity of the effect)".

responding genetic factors. Actually a colony is an assemblage of individuals whose genotype is provided with the same genetic factors. In biform graptolites some of those factors are phenotypically manifested in a part of the individuals only. Hence we may here speak of *incomplete penetrance* of the corresponding genetic factors. In the evolution of many phylogenetic trends we may note that these factors are phenotypically manifested in a progressively increasing number of individuals of a colony. This is the phenomenon of *increasing penetrance* of corresponding factors. Uniform graptolites, produced by these processes, represent forms with *complete penetrance* of corresponding genetic factors.

During graptolite evolution another process is observable, namely that of changes in the extent of phenotypical manifestation of a character (e.g. that of the degree of apertural curvature of hooked thecae, of the degree of overlap of apertural processes or of their asymmetry). This is a process of changes of the *expressivity* of corresponding genetic factors.

In graptolite evolution these two phenomena are distinctly linked. We may always observe here a connection in the spreading of definite characters over a greater number of individuals of a colony (increase of penetrance) and the increase of maximum and mean degree of their phenotypic effect (increase of expressivity). In graptolite colonies the two phenomena are distinctly correlated and expressed according to the spatial pattern of the colony determined by the occurrence of a defined gradient-system. *In graptolite evolution penetrance as well as expressivity are functions of definite morphophysiological gradients.* These are believed to be an expression of the morphogenetic activity of definite genes. In solitary organisms there is no such close correlation of the penetrance and expressivity of definite factors. On the whole, however, strong penetrance is usually associated with strong expressivity of definite genes (Timoféeff-Ressovsky, 1934), though cases of distinct independence of these phenomena have been observed displaying high penetrance and low expressivity or the other way about (Timoféeff-Ressovsky, 1931, 1934). On the other hand, in solitary organisms we know also genes with mutually linked penetrance and expressivity (gene "cryptocephal" in *Drosophila*; Hadorn, 1955). In graptolites genetic changes are manifested so as to suggest a definite spatial pattern. In

Fig. 11. — Diagram illustrating: A-C spreading of a new thecal type introduced proximally into the rhabdosome, and theoretical interpretation of this process, D-F spreading of a new thecal type introduced distally into the rhabdosome, and theoretical interpretation of this process. Further explanations in text.

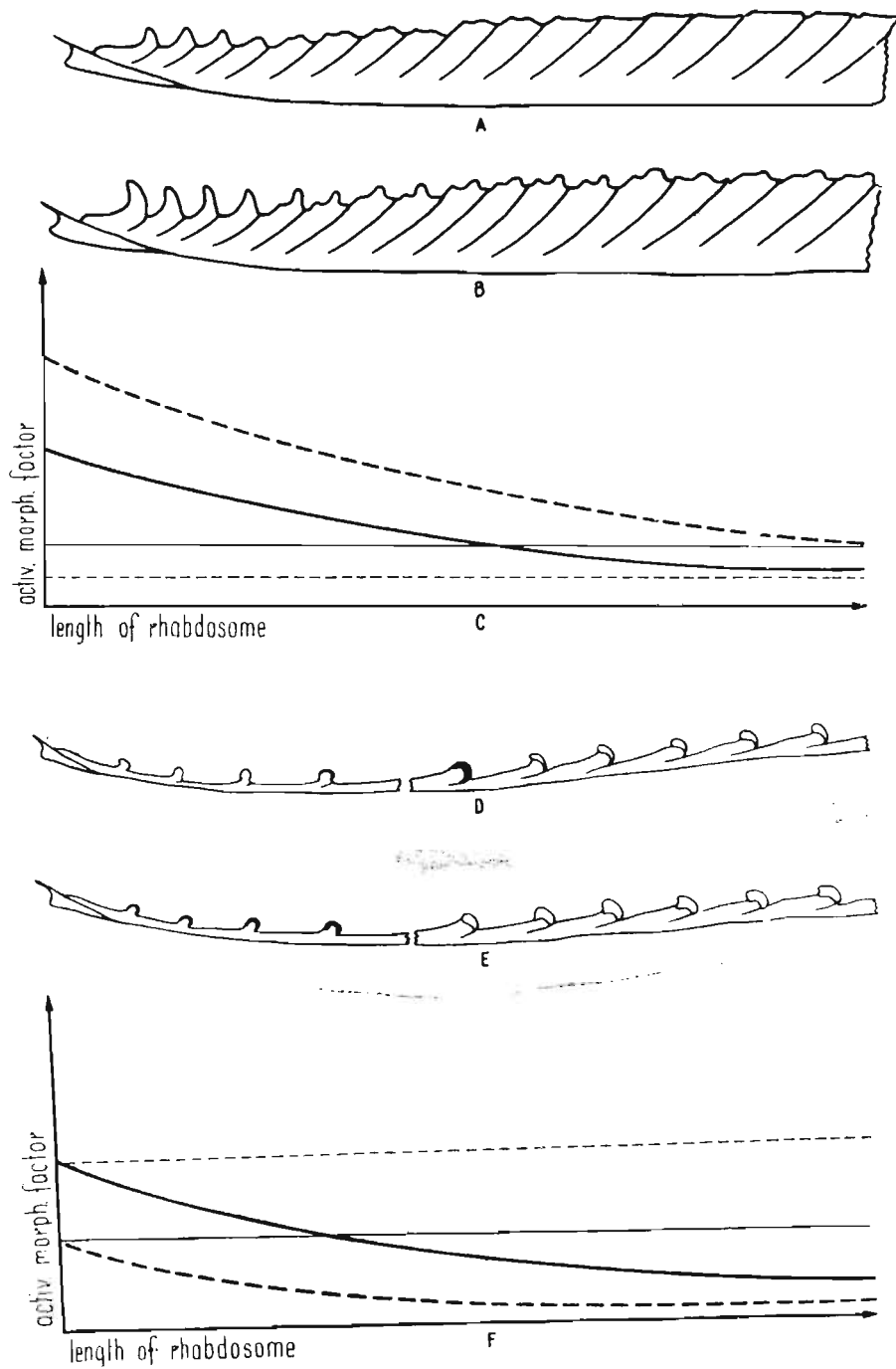


Fig. 11

populations consisting of free-living individuals these processes will usually lack any spatial pattern¹⁹.

The evolution through gradual changes of penetrance and expressivity seems to be the main way of phylogenetic modifications in graptolite colonies. But some known cases do not exclude that particular characters may be manifested simultaneously in all individuals of the colony. This is suggested e.g. by the structure of asymmetric thecae in *Lobograptus scanicus parascanicus* (Kühne) marked by small hypertrophy of the right apertural lobe. No distinct differences in degree of asymmetry is noted between proximal and distal thecae. This form may be regarded as illustrating full penetrance with low and nearly equal expressivity of a factor determining the asymmetry. Nothing can be said presently whether this character was introduced proximally or distally.

The trend of our considerations is diagrammatically illustrated in fig. 11 A-B, representing two successive evolutionary stages in a lineage in which apertural processes have spread out gradually²⁰. This character was introduced proximally into the rhabdosome. In the ancestor it was manifested in some proximal thecae only — A (biform), while in the descendant it spread out over a considerably greater number of thecae and its manifestation was correspondingly stronger in proximal thecae — B (nearly uniform). These changes are explained in diagram C. The curve (thick unbroken line) illustrates the gradient of morphogenetic substance produced by the siculozoid and acting as a stimulator for the considered character. At a certain point this curve intersects the straight line (thin unbroken line) representing the threshold level below which the concentration of the stimulator is no longer strong enough for a phenotypic manifestation of the corresponding character.

The relations shown in fig. 11 B may be interpreted as effect of: 1) the increasing activity of the stimulator (thick broken line), or, when the stimulator keeps a constant level, 2) by the increased activity of corresponding genes intensifying the reaction ability of tissues. This last character would be expressed by a lowering of the threshold level (thin broken line) i.e. by decreasing amounts of the substance necessary for phenotypic manifestation of the given character.

A character introduced distally into the rhabdosome is shown dia-

¹⁹ These differences are not absolute and sharply delimited as is shown by numerous ecologic and geographic gradients (clines), also by others on a different scale, i.e. gradients of sexuality in the assemblages of gastropod *Crepidula* (Hartmann, 1943) etc., which, to a certain extent, are effects of the spatial pattern in populations of solitary organisms.

²⁰ The diagram is based on the evolution ascertained within the group of Saetograptinae (*M.colonus* and *M.chimaera*). Certain details have been here simplified for the sake of better clarity (comp. p. 187).

grammatically in fig. 11 *D-E*²¹. Fig. 11 *D* represents the ancestral form displaying thecal asymmetry within the distal part of the rhabdosome only (biform). This stage is interpreted in diagram in fig. 11 *E*. The curve (thick unbroken line) represents the gradient of morphogenetic substance produced by the siculozoid, which behaves like an inhibitor.

Fig. 11 *E* shows a more advanced evolutionary stage represented by a form with thecae more or less asymmetrical throughout the rhabdosome length and whose expressivity is correspondingly increased distally (uniform). Two alternative interpretations are here suggested: 1) diminished activity of the inhibitor (thick broken line); or, when the inhibitor is at a constant level, 2) increased activity of the corresponding genes expressed by a rise of the threshold level, i. e. an increase of the minimum amount of substance necessary to inhibit the phenotypic manifestation of the corresponding character (thin broken line). In both cases the distribution pattern of the given thecal character and its expressivity are controlled by respective relations of the curve of the gradient decrease and of the threshold value.

An appropriate form of phenotypic manifestation of mutations is supposed to occur in graptolite colonies in connection with their morphophysiological organization evidently characterized by polarity. This manifestation shows regular gradient along the rhabdosome axis. If the penetrance of corresponding genetic factors is incomplete, certain characters are manifested within the colony in a mode indicating a definite spatial pattern, without being randomly dispersed within the colony. The manifestation of a given character is initially strongest in the proximal or distal end of the rhabdosome, gradually fading away towards the opposite end of the colony. The first of the just mentioned alternatives seems to be distinctly more frequent than the other one. Nevertheless it may reasonably be expected that in future we shall obtain more material illustrating the introduction of new characters first affecting the distal end, and gradually spreading over the proximal portion.

*Regularities of evolutionary changes in
graptolite lineages and their genetic significance*

The here suggested hypothesis for the probable genetic mechanisms in the evolution of graptolite colonies calls for verification by actual

²¹ The diagram is based on evolution ascertained within the group of Cucullograptinae. Certain details have been modified for the sake of better clarity (comp. p. 176).

palaeontological evidence. Though the majority of the studied graptolite trends is hypothetical, indeed, even speculative owing to our imperfect knowledge thereof, nevertheless the available material supports this concept. Here below the writer states some more thoroughly examined facts accompanied by conclusions resulting from their analysis.

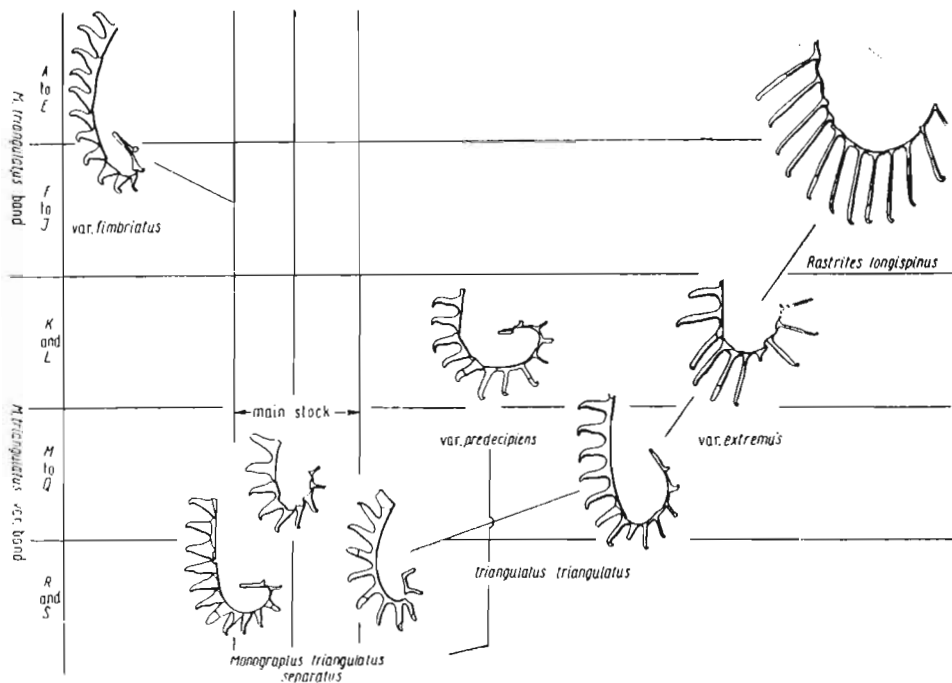


Fig. 12. — Diagram showing evolution of "triangulate monograptids" in lower part of *Pristiograptus gregarius* zone (lower Llandovery, Rheidol Gorge). Note the considerable modifications of thecae in the lineage leading from *Monograptus triangulatus separatus* Sudbury to *Rastrites longispinus* (Perner). A-S successive bands of layers in section (from Sudbury, 1958; specific names actualized).

a) Evolution of "triangulate monograptids"

The evolution of this group is well known thanks to the investigations carried out by Elles (1922), Bulman (1933, 1951) and particularly so from Sudbury's paper (1958). In a very abbreviated form the results of these investigations may be summarized as follows: gradual changes leading from monograptids provided with triangulate distal thecae and rastritiform proximal thecae²² (biform) toward grapto-

²² Such forms have been by Eisel (1911) separated into the genus *Demirastrites* (comp. with remarks on p. 206). According to Bulman (1933) and Sudbury (1958) such forms as the here belonging biform *M. triangulatus* and its varieties come from forms (not adequately known) with triangulate thecae throughout the rhabdosome (uniform).

lites with rastritiform thecae throughout the rhabdosome length (uniform), (*Rastrites*), has been ascertained in succession. The modern investigation approach adopted by Sudbury has, however, permitted to distinguish a number of independent lineages differing in the direction and rate of changes. One of the trends determined by Sudbury (fig. 12) from her so called group "A" "extends from this form²³ through *M. triangulatus triangulatus* (Harkness) and *M. triangulatus extremus* Sudbury to *Rastrites longispinus* (Perner) implying the change from a biform monograptid to a uniform one by way of more extreme biform types. These forms are each different from their ancestor in two ways: a) in having a greater number of rastritiform thecae, and these thecae being more rastritiform; b) in a slight degree of modification of the distal thecae in the same "rastritiform" direction, so that, although the alternation is most marked at the proximal end, each stage really shows a modification acting on the whole rhabdosome, rather than a simple progression of a new character from the proximal to the distal end" (1958, p. 529). And further: „A second line of evolution occurs higher in succession where *M. triangulatus separatus* Sudbury is believed to rise to *M. triangulatus fimbriatus* (Nicholson). Here rastritiform characters of the earlier thecae are lost and they are all triangular. Again the biform *M. triangulatus separatus* Sudbury has produced a uniform type, but the evolution has been in the "opposite" direction — the proximal thecae have lost their distinctive characters and have come to resemble the distal thecae" (1950, p. 529), (comp. fig. 12 and fig. 1 D, B of the present paper).

Group "B" distinguished by Sudbury is represented by several trends, the general direction of their evolution being thus defined by that author: "the dominant trends which can be seen in these series are as follows: 1) loss of overlap in the proximal or in all thecae, 2) increase in the angle of inclination of the thecae to the rhabdosome accompanied by either a) increase in the amount of overlap, or b) complete loss of overlap, 3) reduction in the number of proximal elongated thecae in forms where all overlap is first lost, 4) hooked thecae spread along the rhabdosome, 5) increased dorsal curvature of rhabdosome, 6) a tendency in some cases for the thecae to become transversely expanded at the aperture" (1958, p. 538—539).

The picture of astogenetic evolution in "triangulate monograptid" colonies given by Sudbury fully coincides with our previously sug-

²³ *Monograptus triangulatus separatus* Sudbury. This and the following specific names have been actualized according to Sudbury's note published in the Geol. Magazine, vol. 96, 2, 1959.

gested concepts. The evolution of the first mentioned trends of group "A" (fig. 12) may be interpreted as expressing increased penetrance of genes controlling the "rastritiform" shape of thecae associated with more strongly marked phenotypic manifestation of these characters (expressivity). This process may be understood if we accept that within this evolutionary trend the substance produced by the siculozoid acted as a stimulator of the phenotypic manifestation of the genes controlling the "rastritiform" shape of thecae. Hence the evolution here would consist either 1) in progressively increased activity of the stimulator, or 2) in progressively increased activity of the gene controlling the "rastritiform" shape of thecae, or finally 3) in both these processes.

Somewhat different relations are suggested by the second line of evolution in group "A". Here the most likely hypothesis would be that the action of the stimulator produced by the siculozoid had notably decreased or that reverse mutations had occurred reducing the activity of the gene controlling the "rastritiform" shape of thecae.

The main evolutionary trend in Sudbury's group "B" consists foremost in the spreading of hooked thecae from the proximal end onto the following thecae. This is a typical case of the spreading of a new character introduced proximally. The occurrence of divergent directions in some other characters supports, however, the supposition that spreading of hooked thecae in particular lineages was due to somewhat different factors and that it was stimulated probably through a different complex of genes in each phylogenetic trend.

b) *Evolution of Cucullograptinae*

Sudbury's materials are of notable significance since they permit to trace over a relatively long span of time evolutionary changes in the structure of colonies of immediately allied forms. Some restrictions, however, have been imposed by the state of preservation, since it has been possible to ascertain the nature of shape-affecting changes in forms which have preserved as casts or in semi-relief on the surface of rocks. More suitable in this respect is the material etched by chemical treatment from rocks, mostly boulders of Scandinavian origin²⁴, and lime intercalations in some bore-cores. Fairly numerous forms recovered from these boulders have been described and their morphology thoroughly investigated. An adequate knowledge of the fusellar

²⁴ The monograptids contained in them are, with some exceptions, Lower Ludlovian in age and come mostly from two graptolite zones (*nilssoni* and *scanicus*).

structure, including that of minor details in the structure of thecal apertures, makes this material particularly suitable for genetic analysis. Unfortunately, the stratigraphic sequence of these forms can be only roughly established. Consequently we must handle here certain morphological series whose stratigraphic succession is not known in all details. In spite of these deficiencies the material available to the present author has often proved highly valuable.

The subfamily Cucullograptinae Urbanek, 1958 (fig. 13) seems to be one of the most interesting monograptid groups recovered from erratic boulders. All the forms belonging here are on the whole characterized by a common type of astogeny. They have long, thin, tubular proximal thecae, with long prothecae and very short metathecae: in the course of astogeny they widen out successively, being provided with a sigmoidal ventral wall and a considerably longer metatheca. The forms here referred have the apertural processes fundamentally similar, consisting in simplest cases of two lateral lobes made up of arcuately curved fuselli. During the evolution of this group, however, these processes were subjected to various modifications; therefore, the particular species and their groups belonging here are characterized by strong modifications (comp. genera *Lobograptus* Urbanek and *Cucullograptus* Urbanek). The elaboration of asymmetry is an interesting evolutionary process in this group. Besides the most recently discovered forms, with symmetric apertural lobes (fig. 13 A, B) as the primitive *Lobograptus simplex* n. sp. and somewhat more specialized *L. exspectatus* n. sp., other forms are known with different degree of hypertrophy of the right lobe (*Lobograptus scanicus parascanicus* (Kühne), (fig. 13 C), and *L. scanicus scanicus* (Tullberg), (fig. 13 D) (comp. note on p. 218). Within another evolutionary trend (*Cucullograptus*) we note hypertrophy of the left lobe and dystrophy of the right one (*C. pazdroi* Urbanek, fig. 13 H) or even its atrophy (*C. aversus* Eisenack; fig. 13 F, G). In all these forms thecal structure and their astogenetic succession are fundamentally similar, hence there is little doubt that they are products of the divergence of a common ancestral form, or group of closely allied forms, who had symmetric paired apertural lobes throughout the rhabdosome.

The present writer has lately succeeded in etching out from erratic boulders a form corresponding to the above supposed picture. It represents a new species which the writer proposes to name *Lobograptus simplex* n. sp. The overall thecal structure and astogenetic succession of thecae leaves no doubt but that it is a primitive representative of Cucullograptinae (comp. fig. 13 A, 14 A, 19, 20, and pl. I). The structure

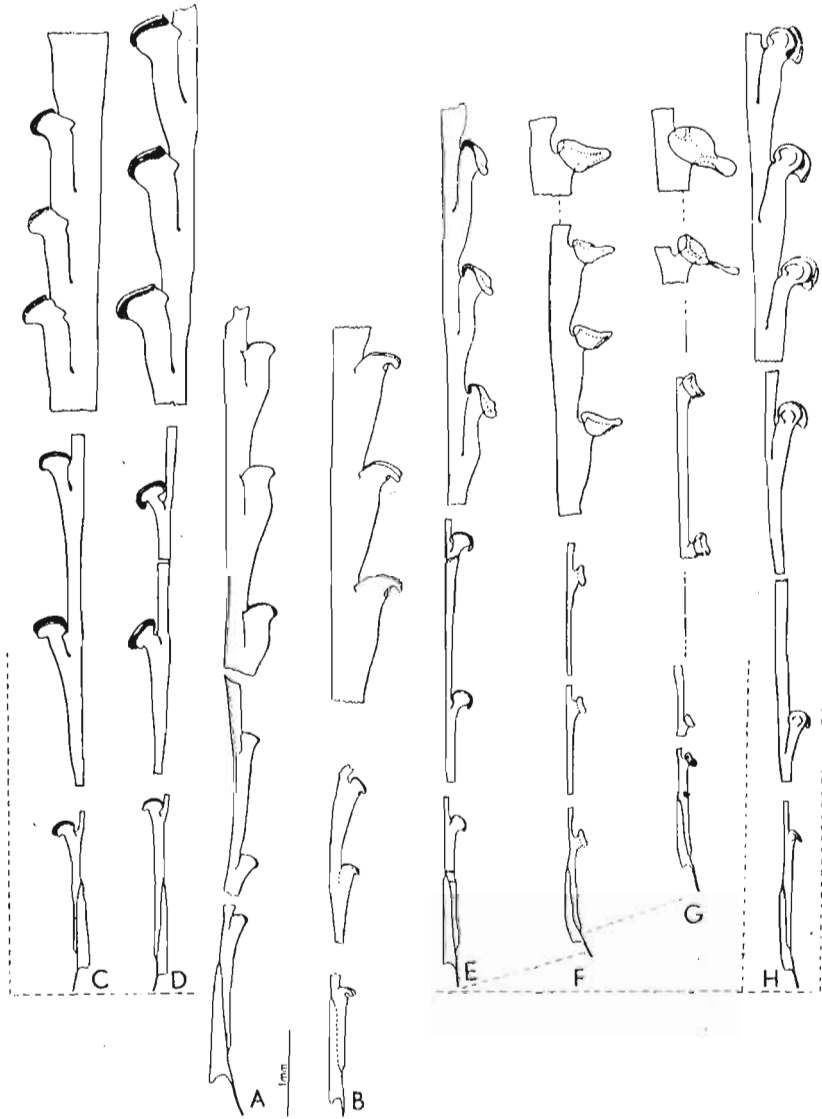


Fig. 13. — Diagram illustrating supposed relationship and astogenetic succession of various Cucullograptinae. For each species or subspecies sicula with th 1, proximal and distal thecae are given. Based on the present writer's material, unless otherwise stated. A *Lobograptus simplex* n.sp., B *L. expectatus* n.sp., C *L. scanicus parascanicus* (Kühne), D *L. scanicus scanicus* (Tullberg), sicula after Walker, 1953; E *Cucullograptus hemiaversus* n.sp., F *C. aversus aversus* (Eisenack), after Eisenack, 1942; G *C. aversus rostratus* n.subsp., H *C. pazdroi* Urbanek. At the top of F and G magnified simple thecae are given to show differences in the structure of apertural apparatus.

of the apertural apparatus is particularly interesting. It consists of two lateral lobes made up of arcuately curved fuselli and somewhat overlapping the aperture. These lobes are of the same size, and do not touch with its free margin, each being separated from the lobe on the opposite

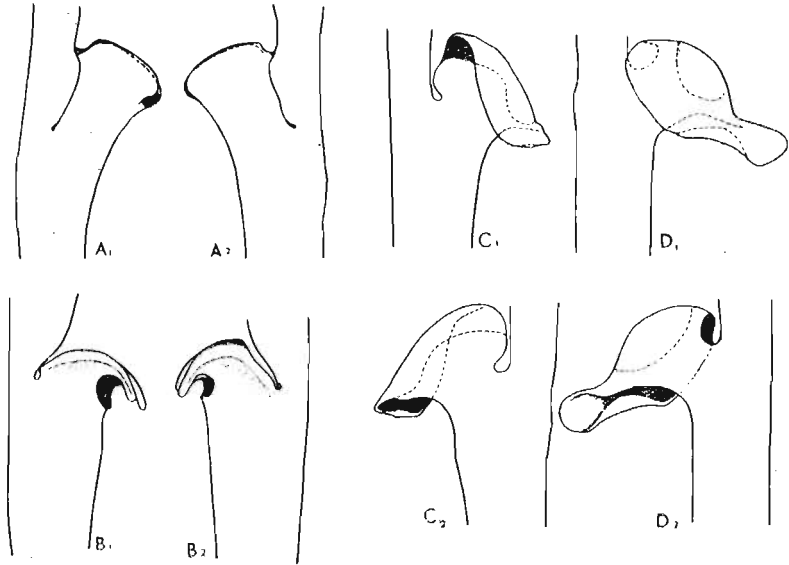


Fig. 14. — Comparison of apertural apparatus of thecae occupying approximately the same position in rhabdosome: A *Lobograptus simplex* n.sp., B *L. exspectatus* n.sp., C *Cucullograptus hemiaversus* n.sp., D *C. aversus rostratus* n.subsp.; 1 right side view, 2 left side view. Increase in size of left lobe, its growing overlap and rudimentation of the right lobe (A, C, D), approx $\times 50$.

side by a distinct fissure (comp. fig. 19 D). Hence no asymmetry pattern is observable. This fact and the fusellar structure of lobes indicate that forms characterized by hypertrophy either of the right or of the left lobe may both be traced back to the just described form. This latter view has been confirmed by the discovery by the present writer of a form which is intermediate between *Cucullograptus aversus* (Eisenack) and *Lobograptus simplex* n. sp. with symmetric apertural processes (fig. 13 E). Forms thus far described may be arranged in a fairly continuous phylogenetic trend whose particular links represent successive stages of astogenetic modifications.

1. *Lobograptus simplex* n. sp. — a form provided throughout the rhabdosome with wholly symmetric apertural lobes, made up of arcuately curved fuselli (fig. 13 A).

2. *Cucullograptus hemiaversus* n. sp. — a form in which the proximal thecae are with nearly symmetric apertural lobes, while the follow-

ing thecae display gradual succession expressed by hypertrophy of the left lobe becoming more or less hood-like and dystrophy of the right one (increase of asymmetry). In the successive thecae the left lobe overlaps the right one which is subjected to partial rudimentation forming a notch on the ventral margin (fig. 13 E).

3. *Cucullograptus aversus aversus* (Eisenack), (Eisenack, 1942) — a form in which thecae on the whole rhabdosome are provided with the left apertural lobe only. This strongly overlaps the right side of theca, while the right lobe displays atrophy and forms only a narrow lip extroverted from apertural margin and covered by left lobe (fig. 13 F).

4. *Cucullograptus aversus rostratus* n. subsp. (described by Urbanek (1954, 1958) as *Cucullograptus aversus*). — From the typical form it differs in stronger overlap of the left lobe, the free margin of this lobe being folded, and in the presence of an outgrowth on the left lobe in medial and distal thecae representing a further stage in the development of the left lobe (fig. 13 G).

Morphological differences between *Lobograptus simplex* n. sp. and *Cucullograptus hemiaversus* n. sp. are stronger than those occurring in the other members of that lineage. It is not out of the question that new forms will be discovered in the future which will fill up a certain discontinuity between these two species²⁵. Even now, however, the presence of symmetric forms intergrading between symmetric *Lobograptus* and *Cucullograptus aversus* suggests that evolution here would consist in the gradual increase of asymmetry and the associated modifications of the apertural apparatus.

This conclusion is apparently confirmed by stratigraphic data (comp. also Appendix, p. 211). *Lobograptus simplex* n. sp. occurs in an assemblage suggesting the *scanicus* zone, as currently defined, most probably its lower horizons or boundary with the *nilssoni* zone. *Cucullograptus hemiaversus* n. sp. occurs in an assemblage suggesting the *scanicus* zone (presence of *chimaera* group), but the lack of true *scanicus* in its assemblage may suggest rather higher horizons of this zone. This is confirmed by the fact that in a bore-core (deep-boring Mielnik, Eastern Poland) forms determined as *C. cf. hemiaversus* and preserved in semi-relief on rock surfaces occur at depth of 953 m, just above the top of the *scanicus* zone as currently defined. Zone of occurrence for *Cucullo-*

²⁵ German palaeontologists Dr W. G. Kühne and Dr H. Jaeger (Berlin) are in possession of material representing similar and identical forms which, to a certain extent, probably complete the here presented picture of the evolution of the *Cucullograptinae*.

graptus aversus aversus (Eisenack) cannot be determined more precisely; it was described by Eisenack (1942) in association with *Pristiograptus frequens* Jaekel, being most probably a junior synonym of *Pristiograptus dubius* (Suess), (comp. Kühne, 1955). Scarcity of associated forms in erratic boulders and lack of *scanicus* also suggest a horizon above the true *scanicus* zone. Still higher horizons are suggested for *Cucullograptus aversus rostratus* n. subsp., which was found in limy intercalations in the core of deep-boring Mielnik, at depth of about 920—925 m, approx. 9 m above the zone of occurrence of *M. cf. leintwardinensis* (Hopkinson), and 15 m above the last appearance of *Saetograptus chimaera cf. salweyi* (Hopkinson), and some 30—35 m above the *scanicus* zone proper! The stratigraphic succession of these forms, although their first appearance cannot be fixed precisely, seems to fully agree with the postulated morphological sequence²⁶.

Hence in this group evolution consisted in gradual modifications of thecae and in astogenetic changes. Only slight morphological differences of the 3 successive members of that trend (2—4) suggest that we are dealing here with a continuous evolution ("gleitende Evolution"). A continuity of evolution is indicated also by small but distinct differences existing between populations of *Cucullograptus aversus rostratus* n. subsp. from particular samples: degree of overlap, size and bending of outgrowth on left lobe, slight increases in populations from boulders S. 121 and S. 205, the expressivity of these characters being the strongest in sample from bore-core Mielnik, at its higher horizons (comp. p. 217). The morphological differences of the particular forms here regarded — conformably with the accepted practise — are ranked as corresponding to specific or subspecific level. The question whether they are to be recognized as separate species or subspecies only is a purely academic problem without any real bearing on the here considered matter.

Forms representing these successive evolutionary stages are expressed by: 1) spreading of asymmetric thecae characterized by hypertrophy of the left lobe, from the distal to the proximal end of rhabdosome (character introduced distally); 2) stronger expression of characters of these thecae manifested by increasing maximal degree of overlap and folding of the free margin of the left lobe; 3) dystrophy or reduction of the right lobe, depending on the degree of hypertrophy of the left lobe; 4) further development of the left lobe, expressed by formation of an outgrowth on this lobe in distal thecae of *Cucullograptus aversus*

²⁶ Distribution of remaining *Cucullograptinae* cited above may be defined as the *scanicus* zone, or probably this zone.

rostratus n. subsp. The latter character is lacking in proximal thecae, being evidently introduced distally into the rhabdosome.

An analysis of morphological changes and of astogeny in this evolutionary trend of monograptids leads to interesting conclusions as to the probable nature of genetic changes. It provides convincing evidence proving that the evolution of graptolite colonies occurs in way of increased penetrance and expressivity of genetic factors among individuals of a colony. The more strongly asymmetric are thecae, the greater is the number of individuals in a colony affected by it. Within the Cucullograptinae group colonies primarily consisted of symmetric thecae only (*Lobograptus simplex* n. sp.; fig. 13 A, 14 A), ("uniform"), later asymmetric thecae appeared in the distal and medial portion (*Cucullograptus hemiaversus* n. sp. — "biform" — incomplete penetrance), (fig. 13 E, 14 C), subsequently to involve the whole rhabdosome (*C. aversus* — "uniform" — complete penetrance), (fig. 13 F), and again secondarily "biform" through the presence of outgrowth on left lobes in more distal thecae of *C. aversus rostratus* n. subsp. being a new character introduced at distal end of rhabdosome (fig. 13 G, 14 D). The maximum phenotypic effect increased simultaneously, e.g. the extent of overlap of the free margin in the left lobe and its folding in given thecae increases in a number of these forms (comp. fig. 14 A, C, D), i. e. the expressivity of the character grows stronger.

Similar relations have been ascertained by Sudbury (1958). Within a group of species passing from *M. triangulatus separatus* Sudbury to *Rastrites longispinus* (Perner) we may observe a gradually increasing number of rastritiform thecae in which the rastritiform character becomes progressively more strongly manifested. The more strongly rastritiform are the thecae, the greater is the number of individuals in a colony manifesting this character (fig. 12).

In the lineage of *Lobograptus scanicus*, however, thecae do not distinctly differ in degree of their asymmetry. These forms may be regarded as nearly uniform in this respect and representing full penetrance and rather low expressivity of factor determining asymmetry. Nothing can be presently said whether hypertrophy of the right apertural lobe was a character introduced proximally or distally (comp. also p. 172).

An analysis of development of the asymmetric Cucullograptinae suggests further interesting genetic implications. The asymmetry in the lineage of *Cucullograptus aversus* results from hypertrophy of the left apertural lobe. The right lobe is subjected to rudimentation determined by the size and degree of overlap of the left lobe onto the right one.

We are probably dealing here with antisymmetric manifestation of determined genetic factors. These are supposed to consist in such phenotypic manifestation whose occurrence in one of the antimeres excludes the occurrence of effect in the other antimer (Timoféeff-Ressovsky, 1934). In *Cucullograptinae*, however, we are dealing not only with antisymmetry which excludes the bilaterally simultaneous manifestation of the given factor, but also with determined antisymmetry which causes the given character to affect a determined antimer only. This consists of hypertrophy either of the right side of the zooid alone (*Lobograptus scanicus*) or of the left side (*Cucullograptus*). In the presence of two, symmetrically placed lobes, this factor has the potential ability of bilateral manifestation, actually however it affects one of the lobes only. We must infer that different factors determining the symmetry type and the mode of the manifestation of mutations must have occurred in the above mentioned phylogenetic trends. The whole genotype, probably substantially different in the two groups, may be regarded to represent these factors. Genetic data indicate that the mode of manifestation of determined genetic factors in relation to symmetry is controlled by hereditary factors (Astauroff, 1929; Timoféeff-Ressovsky, 1934) and may be altered under the action of artificial selection. This throws some light on the supposed genetic mechanisms which have determined the type of antisymmetry that has stabilized within the particular trends of *Cucullograptinae*.

From the morphophysiological viewpoint it is most probable that the asymmetric structure of the apertural apparatus in *Cucullograptinae* reflected the asymmetric shape of the soft organs of the zooid, particularly so of the lophophore arms. When comparing these processes with similar ones in living organisms we see that reduction of a certain number of analogous organs is in most cases compensated by hypertrophy of the remaining ones which complement their physiological function. An interesting illustration of this phenomenon is provided by hydrozoans in which the number of tentacles may be reduced to two or even one (*Lar sabellarum* and *Monobrachium parasiticum*; Dogel, 1954). Organs subjected to numerical reduction (oligomerization) may, subsequently, be subjected to secondary compensating development, "polymerization", hypertrophy or ramification (Dogel, 1954). The most likely hypothesis here would be that claiming the occurrence within *Cucullograptinae* of mutations responsible for some degree of reduction of the lophophore. These mutations occurred either on the left side (*Lobograptus*) or on the right side (*Cucullograptus*) causing a correspondingly compensating hypertrophy of the opposite side of the lophophore. Depending on the varying "gene environment" in which they were

expressed or, on their different character in the particular phylogenetic trends these mutations were more or less strongly manifested either on the left side (*Lobograptus*) or on the right side (*Cucullograptus*). This would be an expression of pseudopletiotropy, i. e. the effect of mutations on a number of correlated characters. Actually it could only be the expression of certain regulating processes manifested during the growth of the zooid. In that case, atrophy of the right lophophore would result in correspondingly strong hypertrophy of the right lophophore in order to accommodate it (lineage of *C.aversus*). The whole complex, therefore, of modifications affecting the apertural apparatus would be the result of one mutation with strong "pleiotropic" activity. This may be explained as a chain of mutually linked correlations, in which changes of one organ cause the corresponding changes in another organ (Šmalgauzen's morphogenetic correlation, 1946)²⁷.

c) *Modifications of astogeny in diplograptids*

A most interesting picture of directional changes is provided by phylogenetic series known in numerous diplograptid lineages with gradually modifying thecal budding. The most suggestive observations made by Davies (1929) and Waern (1948), (comp. p. 164), will be here discussed and interpreted more at large.

Davies has with some details described this process in *Glyptograptus* aff. *persculptus* (Salter). Mutations of this species collected from successive horizons of the Ystradffin section, Carmarthenshire (Wales), are represented by forms in which the median septum is gradually shortened on the reverse side, while the number of thecae with alternating budding is consequently increased. Davies' data are diagrammatically shown in fig. 15. On the X-axis thecae are shown at whose level the median septum begins in the successive mutations. The first 5 mutations are represented by forms from Ystradffin (*Glyptograptus persculptus* zone), the 6th by one from Torver Beck in the Lake District. These mutations represent forms with different degree of biformism in respect of the mode of budding. However, in the top of the higher zone with *Akidograptus acuminatus* (Nicholson), Davies has noted the presence of forms (mut. *omega*) probably lacking the median septum (uniform in respect of the mode of budding).

The resulting morphological and stratigraphic succession is a very suggestive one. The successive mutations are characterized by an increasing number of alternately budding thecae and a corresponding

²⁷ A detailed analysis of the structure of forms belonging here and of their evolutionary changes will be given in the writer's paper just preparing.

shortening of median septum on the reverse side (fig. 15). This character was introduced proximally and gradually spread distally in a series of forms constituting the successive evolutionary stages, suggesting a certain polarity of the rhabdosome in this respect too. The activity of the factor controlling the alternate budding of thecae was gradually

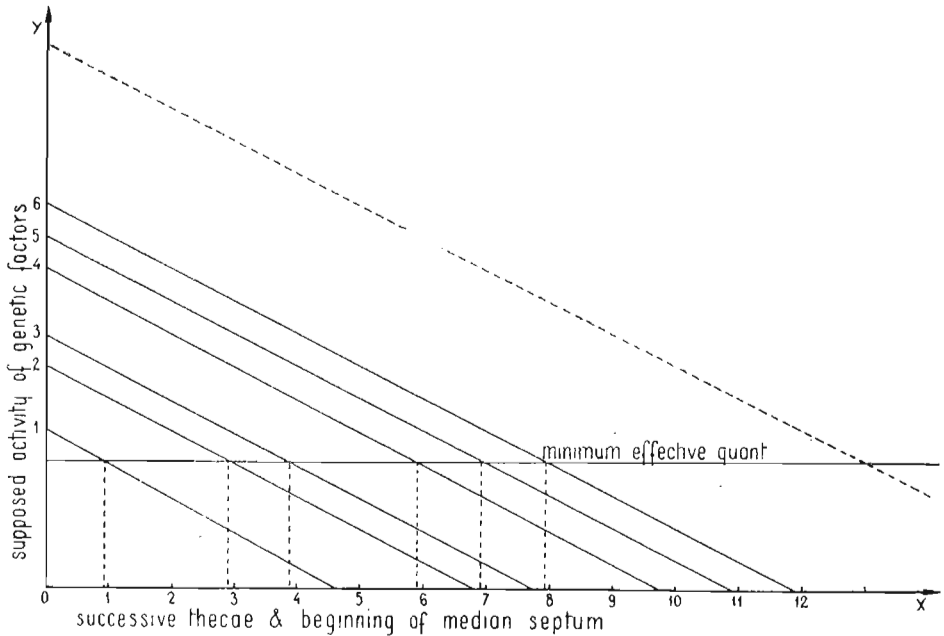


Fig. 15. — Interpretation of progressive shortening of median septum in the lineage of *Glyptograptus* aff. *persculptus* (Salter), (data after Davies, 1929). In 6 successive zonal mutations median septum begins at the point where effectiveness of corresponding morphogenetic factor decreases below the threshold value (line parallel to X-axis). Further explanations in text.

increased in the evolutionary lineage. Values indicated in the Y-axes in fig. 15 are proportional to their morphological effects, i.e. to the number of alternating thecae, and at the same time represent the relative activity of factors determining the mode of budding. In graptolite colonies the factor responsible for the mode of budding would display a certain gradient along the rhabdosome. Where the amount of the required substances drops below a certain threshold level (thin line parallel to the X-axis), two independent thecal series are supposed to begin, separated by the median septum. When the activity of genetic factors is sufficiently strong, the rhabdosome will be aseptal throughout its length (broken uppermost line).

The observations of Waern (1948), based on data from the Kullatorp boring, Kinnekulle in Vestergötland, Sweden, are very much analogous. He

has ascertained that "*Climacograptus scalaris* v. *transgrediens* forms a transition between *Cl. scalaris* v. *normalis* and *Cl. medius* with regard to the time of its appearance as well as to its anatomical characteristics. *Cl. scalaris* v. *transgrediens* occurs simultaneously with and somewhat

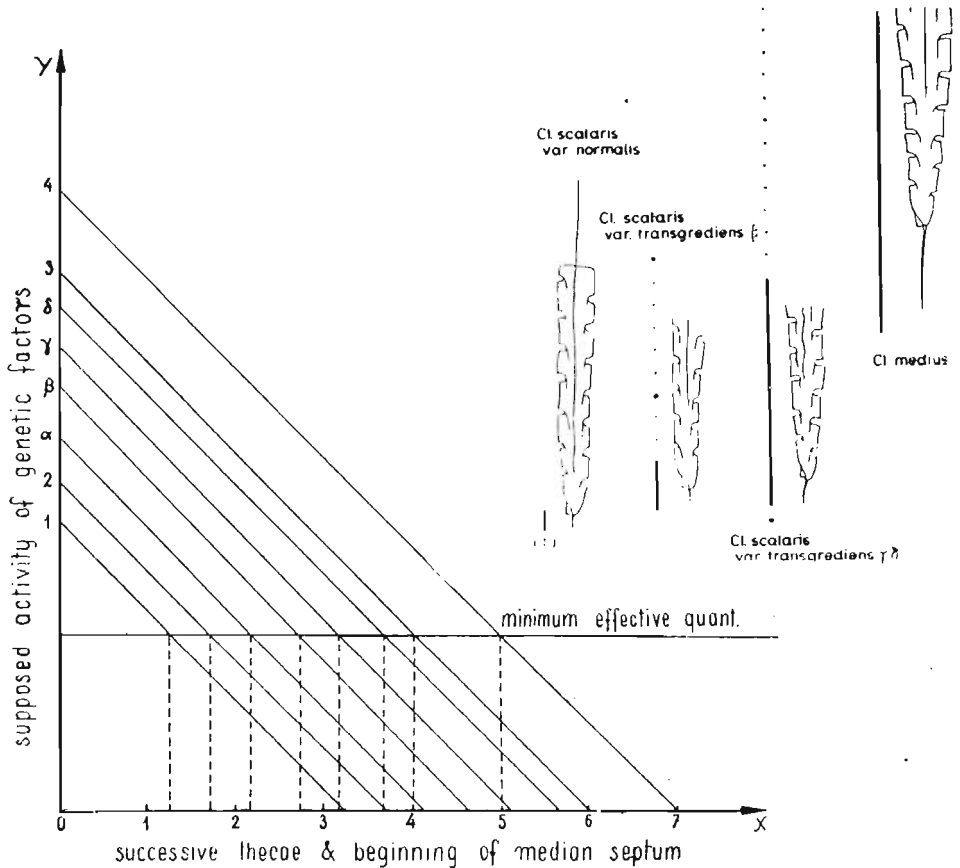


Fig. 16. — Interpretation of progressive shortening of median septum in the lineage of *Climacograptus scalaris* var. *normalis* Lapworth (data after Waern, 1948). 1-2 relative values for *Cl. scalaris normalis* for successive zonal mutations of *Cl. scalaris transgrediens* (α - δ), 3-4 for *Cl. medius*. Further explanations in text and fig. 15. Upper right corner — corresponding zonal mutations and their distribution in the bore-core (from Waern, 1948).

later than *Cl. scalaris* v. *normalis*, first forma α appears, then forma β , γ and the last surviving specimens are contemporaneous with the earlier occurrence of *Cl. medius*" (p. 450), (comp. fig. 16 of the present paper).

Data concerning the shortening of median septum on the reverse side of rhabdosome are particularly interesting. Waern's measurements are shown diagrammatically in fig. 16. That author did not only ascertain

the theca at whose level the median septum arises on the reverse side, but moreover indicated the exact point of its beginning in per cent figures of thecal length. Waern's data, though based on 30 specimens only, seem to be quite reliable. Mean values (Waern, 1948, p. 450) have been used by the present writer to plot the diagram. The progressive delay in formation of median septum on the reverse side in successive forms is shown on the straight line parallel to the X-axis illustrating the constant threshold level. The delay is referred to the activity of the corresponding genetic factor (Y-axis). This results in a picture very similar to that provided by the here above described example of *Glyptograptus* aff. *persculptus* (Salter).

Both these examples clearly show the process whose successive stages seem to have been caused by fundamentally analogous factors, with gradually increasing activity, causing the appearance and gradual spreading of a new mode of budding. The only factors that may actually be here taken into account are changes of multiple-factors (modifiers) acting as stimulators of a certain basic gene controlling the alternate budding of thecae, or a multiple alleles series of a "major gene" responsible for the directional changes of the activity of a determined factor and for the reactivity of tissues²⁸.

d) Evolution in *Saetograptinae*

An interesting example is provided by the evolution of apertural processes in subfamily *Saetograptinae* Urbanek, 1958, represented by two Ludlovian genera: *Colonograptus* Přibyl and *Saetograptus* Přibyl. A typical representative of the former genus (*Colonograptus colonus* (Barrande)) is characterized by the presence of paired apertural processes on proximal thecae (first 3—4 thecae), which are triangulate ear-like structures (fig. 17 a, b). The following thecae are provided with a rather small elevation on the apertural margin only, while beginning with thecae 14-15 the margins are perfectly smooth and thecae simple, "pristiograptid". Such forms may be regarded as representatives of the "biform" type (comp. fig. 2 C). In a typical representative of the other genus (*Saetograptus chimaera* (Barrande)) the thecae are, on the whole rhabdosome length, provided with apertural processes. In proximal thecae (first 9—10 thecae) these are in shape of long spines,

²⁸ In connection with this problem, Davies has made another interesting observation (192^a) that in *Glyptograptus* aff. *persculptus* it "is interesting to note that the mutations at higher horizons are much more uniform in nature and the variation between specimens from same bands typical of the lower horizons is not seen" (p. 14). This might have been associated with a kind of variability reduction, noted in many other groups too, and by Simpson (1944, 1955) explained as result of natural selection.

gradually shortened in the next thecae to an elevation of apertural border in distal thecae (comp. fig. 2 B, and 17 d-j). In many respects these genera are similar enough to be regarded as closely allied (Přibyl, 1942, and particularly Urbanek, 1958, here modified according to new available data).

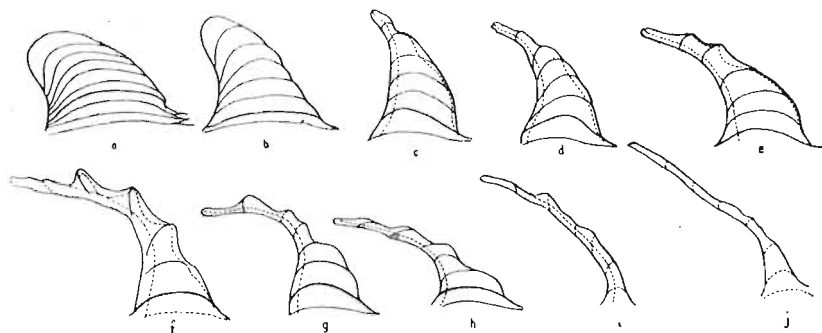


Fig. 17. — Series of apertural processes in Saetograptinae representing successive stages of reduction of their peridermal membrane: a-b *Colonograptus* cf. *colonus* (Barrande), c transient between *Colonograptus* and *Saetograptus*, d-e *Saetograptus chimaera chimaera* (Barrande), (in sense of Urbanek, 1958), f *S.chimaera cervicornis* Urbanek, g-h *S.chimaera* cf. *cervicornis* Urbanek, i-j *S.chimaera* cf. *salweyi* (Hopkinson). Borders between the processes and their basis marked by thick line, borders of fuselli, when uncertain or conjectural, marked by broken lines. All processes represent the 1 of young rhabdosomes (boulders S. 19, S. 36, S. 38, S. 54, S. 149, S. 201), approx. $\times 50$.

Stratigraphic evidence concerning Europe indicates that *Colonograptus* appeared earlier. It was present in the lower part of the Lower Ludlovian *nilssoni* zone, while forms referred to *Saetograptus* did not appear before the uppermost part of the *nilssoni* zone and are typically present in the higher *scanicus* zone (Great Britain: Elles & Wood, 1901—1918; Boswell, 1926, 1928; Blackie, 1928; Lawson et alii, 1954; Barrandian: Horny 1958; Holy Cross Mountains, Poland: Tomczyk, 1956; Thuringia, Germany: Jaeger, 1959). Within the particular regions the faunal succession of the Lower Ludlovian assemblages differs slightly but it seems quite safe to generalize that *Colonograptus* made its appearance earlier than *Saetograptus*.

The available data very clearly suggest that evolution occurred by gradual changes from forms with apertures of the *Colonograptus* type to those with apertural spines of the *Saetograptus* type. Forms belonging here and etched by the present writer from erratic boulders of Scandinavian origin may be arranged in a continuous morphological series mutually differing in modifications of apertural processes (fig. 17).

These modifications are affected through reduction of the surface of apertural processes owing to: 1) tubular folding of the anterior margin of the process (Urbanek, 1953, 1958), 2) reduction of the posterior margin, surrounding the more protruding lappets of the apertural process. The latter are placed on the lines of contact between the particular fuselli, constituting a kind of frame for particular lappets. The reduction of the process may continue along this line until the complete disappearance of the free peridermal wing of the process which persists merely as fine hair-like rudiments only. These elements constitute a strongly attenuated membrane folded into a tubule. The formation of such tubule-like peridermal structures is a form of rudimentation of the fusellar periderm. They occur in other graptolites (e.g. in *Cucullograptus hemiaversus* n.sp. and *C.aversus rostratus* n.sp., where the reducing and attenuated portion of the right apertural lobe is altered into a tubular lip of this kind, extraverted on the margin of aperture).

In fig. 17 processes of th 1 all belonging to young rhabdosomes in stages 1-4 thecae are shown for a better comparison of their structure. This permits to avoid the effect of possible secondary changes due to thickening of the periderm owing to the superimposition of the additional substance. The fusellar structure of the processes could be sufficiently well examined in most cases. Broken lines indicate poorly discernible or conjectural fusellar boundaries.

The series shown in fig. 17 is readily explained as an expression of the gradual reduction of the peridermal membrane due to inhibition of peridermal growth. Hence, the anterior margin, formed by the secondarily attenuated membrane, is folded (probably owing to mechanical factors) below the thicker portion of the periderm, while the posterior margin is reduced first by the formation of a number of incisions, later on by complete reduction of periderm. Wherever this process manifested stronger activity (first 3 thecae in *S.chimaera cervicornis* Urbanek and their greater number in *S.chimaera* cf. *salweyi* (Hopkinson)), we note strong destruction of the periderm, and more spine-like processes. Where the process did not attain such intensity, it was manifested merely in the narrowing of the surface of peridermal membrane of the processes (fig. 17 b, c). The various forms shown in fig. 17 are referable either to the genus *Colonograptus* (fig. 17 a, b) or to genus *Saetograptus* (fig. 17 d-j), or they represent morphological transients (fig. 17 c). Forms shown in fig. 17 a, b occur in an assemblage probably suggesting the lower *nilssoni* zone, those shown in fig. 17 f-h, j in an assemblage indicating the overlying *scanicus* zone, while horizons

in which forms fig. 17 *c-e* and *i* occur cannot be more exactly identified²⁹.

It is, however, quite doubtless that these are closely allied forms belonging to the same evolutionary trend. This is, moreover, confirmed by the fact that, wheresoever it has been possible to ascertain, the free part of the process protruding above the apertural margin is invariably made up of the same number of fuselli (6). Where this number could not be quite surely determined, the possible deviation ought not to exceed ± 1 . The strikingly stabilized structural pattern of processes apparently indicates that in this trend structure of apertural processes was genetically controlled and that its possible zonal variations occur in the way of mutation. The more thoroughly studied geological sections of the Ludlovian all seem to confirm that forms with the *Colonograptus* type of process did, indeed, appear earlier and are associated with the lower part of the *nilssoni* zone, while forms with more or less reduced periderm of processes of the *Saetograptus* type are associated with the higher part of that zone and with the upper *scanicus* zone. No reliable evidence, however, is available as to whether the latter forms (*Saetograptus*) are contemporaneous or whether they attained dominance in successive horizons from the lower to the higher. Material recovered from erratic boulders does not provide sufficiently detailed stratigraphic data, while material known "in situ" does not, on the whole, permit the distinction of such subtle differences in the shape of apertural processes³⁰.

It is, however, rather noteworthy that besides boulders containing forms representing various reduction stages (e.g. fig. 17 *c-e*, from

²⁹ The assignment of the various boulders to corresponding graptolite zones on their graptolite assemblages is to a certain extent arbitrary. Actually, the changes in faunal composition are gradual and at the boundary of two horizons index forms and associated fauna are often encountered, characteristic of both the lower and the higher horizons. This is suggested by many statements and data of various authors, particularly so Elles & Wood, 1901-1918; Boswell, 1920, 1928; Blackie, 1928; Hede, 1942; Lawson et alii, 1954. On the other hand, the absence of a given index form from a boulder may be also merely random, because they hardly are really representative samples of a determined horizon.

³⁰ There is some evidence, however, showing that *Saetograptus chimaera salweyi* (Hopk.), though very likely representing the most advanced morphologic stage, is to be encountered already in the upper part of the *nilssoni* zone. Subsequently it passes into the *scanicus* zone, occurring there together with the type form and with its other varieties (Boswell, 1926, 1928; Blackie, 1928). The typical form *S.chimaera chimaera* (Barrande) is also reported from the *nilssoni* zone (Elles & Wood, 1914). The picture became more complicated by the data of Elles (1944) who indicates at least two mutations of *salweyi* — "limp" one from *nilssoni* zone and "rigid" one from higher beds (*scanicus* zone — base of *leintwardinensis*). Probably there are some local stratigraphic differences and both these forms of *S.chimaera* were presumably more or less contemporaneous, the *salweyi* surviving longer.

boulder S. 54) there are others in which one particular type of process dominates. These would probably correspond to populations with a determined genetic structure (Urbanek, 1958). The time succession of these forms suggests that we are here dealing with an evolutionary process. Hence this series of processes cannot be explained by the direct influence of environmental factors, though occasionally they do cause modifications giving the semblance of genetic changes (Goldschmidt (1938) described these phenomena in respect to the various mutations of *Drosophila*). A direct environmental influence may have, however, intensified the range of variability of the forms here.

When analysing changes occurring in this evolutionary trend we will be able to conclude that differences between *Colonograptus* and *Saetograptus* consist of: 1) structural changes in the apertural processes, the peridermal membrane of processes in *Saetograptus* being reduced gradually; 2) numerical increase of thecae provided with processes, i.e. of proximal thecae in *Colonograptus* Přibyl and throughout the rhabdosome in *Saetograptus* Přibyl. The maximal length of processes increases too.

The first process results in a morphological picture very much like that of the destruction of wing chitine in the series of multiple alleles — "vestigial" in *Drosophila* (fig. 18). There too, reduction occurs owing to the formation of local "marginal incisions" between the nervures on the wing surface. According to Goldschmidt (1938 and earlier) who has examined the developmental mechanism of these changes, the wings in mutants first develop quite normally. Later on in a stage determined for each mutation, the chitine is subjected to resorption or to lytic processes. Wings are thus formed, displaying a varying extent of scalloping. The reduction of wing chitine in a "vestigial" series is by Goldschmidt (1938) explained as the manifestation of various activity of particular alleles in the production of a substance necessary for the normal development of wings or in the formation of lytic substance displaying a localized specific action.

The second process may be readily explained by the hypothesis that the penetrance (number of thecae provided with processes) and expressivity (length of processes) of genetic factors responsible for the origin of processes had been increased in that evolutionary trend. In *Saetograptus* we would be dealing, however, with a certain state of equilibrium between factors determining the degree of penetrance as well as the expressivity of apertural processes and those controlling the extent of the destruction of periderm in processes. Hence the relations here are apparently more complex than those described in

regard to the reduction of wings of *Drosophila* in the "vestigial" alleles series (Mohr, 1932; Goldschmidt, 1938). There it had been possible to ascertain the direct relation between the penetrance of one allele and its potency expressed in the degree of destruction of wings (degree

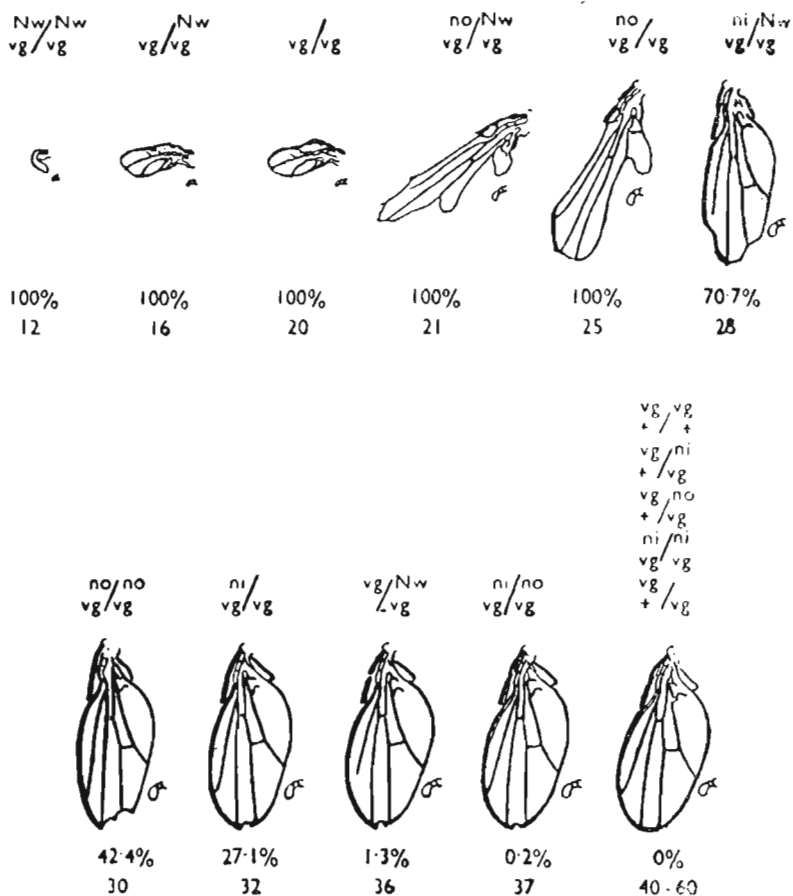


Fig. 18. — A series of modal phenotypes of the wings and balancers in all diploid combinations of the allelomorphs of "vestigial" in *Drosophila melanogaster*, as an example of directional effect of multiple allelomorphs: *nw* no wing, *vg* vestigial, *no* notched, *ni* nicked, *+vg* wild type. Percentage of penetrance and relative value of activity for each combination given below (after Mohr, 1932).

of phenotypic effect, comp. fig. 18). In our problem it is hardly to be supposed that the same genetic factors are responsible for both these processes, particularly since they are physiologically opposite (formation of processes — reduction of processes) and more or less independent in their activities. Most probably at least two independent factors are here involved. *We may simultaneously observe here the high penetrance*

of the factor responsible for the presence of apertural processes and the manifestation of the factor determining the reduction of the membrane in these processes (*Saetograptus*). Among the many possible interpretations of this doubtlessly complicated phenomenon, the simplest one would be that accepting a certain state of dynamic balance of genes, analogous to the state of "epistatic minimum" in sex determination of gypsy moth — *Lymantria dispar* (Goldschmidt, 1938). In these graptolites this would correspond to the stage in which the penetrance of the gene, responsible for the formation of processes, is sufficiently high, while the simultaneous fairly active manifestation of destruction processes of their periderm is determined by other genetic factors.

In this trend similar changes in the penetrance of genes might have been an important factor controlling the astogenetic succession of thecae. E. g. we know certain forms described as separate species or subspecies, such as *Saetograptus chimaera semispinosus* (Elles & Wood) in which only some proximal thecae are provided with apertural spines lacking in the distal thecae of the rhabdosome. This form has been recorded from the *scanicus* zone. Similarly, *Colonograptus varians* (Wood) from the *nilssoni* zone is characterized by the low penetrance of the factor responsible for the formation of apertural processes. We may reasonably expect that, in case of further reduction of the penetrance, the just mentioned forms might give rise to forms completely lacking apertural processes. This stage might not even necessarily mean the occurrence of amorphic mutations of the corresponding gene but result from the action of modifiers. In connection therewith it is interesting to note differences in the number of thecae provided with apertural processes (retroverted thecae) in *Colonograptus varians* from various localities in the Long Mountain District, where they are provided with one, two or even three of such thecae (Elles & Wood, 1914). They would correspond to differences of penetrance of definite mutations in stocks from various areas (Timoféeff-Ressovsky, 1934). The relations here match best those in the mutation of *venae transversae interruptae* (vti) in *Drosophila funebris*. In some of its stock this mutation is not phenotypically expressed. Its phenotypic manifestation occurs solely in the presence of some other mutations acting as modifiers and occurring in certain races only with a definite geographical distribution.

e) *Supposed genetic mechanisms of evolutionary changes in graptolite colonies*

The here above discussed cases of evolution in several phylogenetic graptolite lineages clearly indicate that their development passes from

primarily uniform forms, through various stages of biformism, to forms secondarily uniform. An example of such processes is the evolution of monograptids towards the genus *Rastrites* Barrande. It is assumed that it led from "uniform" graptolites having triangulate thecae on the whole rhabdosome, through forms with varying degree of biformism to species provided with rastritiform thecae throughout the rhabdosome length, i. e. to secondarily uniform forms (Sudbury, 1958). Similarly, among *Cucullograptinae*, forms originally uniform (*Lobograptus simplex* n. sp., with symmetric apertural apparatus on the whole rhabdosome) may lead to biform species (*Cucullograptus hemiaversus* n. sp., with asymmetry of apertural apparatus in distal and medial thecae), and from these — to species in which the apertural apparatus is asymmetric throughout the rhabdosome length (*Cucullograptus aversus aversus* (Eisenack)) — secondarily uniform. In the next stage the rhabdosome becomes secondarily biform through introduction at the distal end of a new character in *Cucullograptus aversus rostratus* n. sp.

Hence, the difference of primarily uniform forms from the biform ones lies in the appearance of a new character, i. e. the occurrence of corresponding mutations. On the other hand, the difference of biform forms and their secondarily uniform descendants consists in the degree of spreading and manifestation of corresponding features which, as is shown, may be regarded as an effect of various expressivity and penetrance of the corresponding genetic factors.

Thus, biform graptolites may be regarded as species with genetically controlled incomplete penetrance of definite genetic factors, while the corresponding secondarily uniform forms would be considered as species with genetically controlled complete penetrance of definite genetic factors.

In graptolites, whose evolutionary process passes through these two stages, new mutations would initially produce alleles with low phenotypic expression. The activity of their phenotypic manifestation would increase in the course of evolution³¹. For certain forms, however, the

³¹ The increasing activity in the phenotypic manifestation of corresponding genetic factors in graptolite colonies to some extent suggests analogies with the process of evolution of genetic dominance. The latter process may be understood either as an expression of the selection of corresponding modifiers (Fisher et alii), or that of stronger activity of the same "basic" gene (Wright et alii), (comp. discussion in Smalgausen, 1946; Wagner & Mitchel, 1955). Relations prevailing in the evolution of a graptolite colony answer well the gradual changes which must have affected activity of each definite genetic factor first manifested as semidominant and later becoming fully dominant. These data seem to represent sound evidence for Goldschmidt's statement (1946) that "the evolutionary process begins with mutants of low penetrance and expressivity", but have no distinct relation to his supposition that this mutation must necessarily be a "large" one (comp. Simpson, 1953).

biform stage may have meant stabilized conditions and not a transition towards secondary uniformism. Bulman e. g. believes that *Monograptus decipiens* Törnquist is one of these species.

Though we have seen that in many phylogenetic graptolite lineages evolutionary changes are expressed by gradual spreading of the new thecal type, it is not impossible that other mutations may occur at once characterized by complete penetrance, i. e. those spreading simultaneously over all the individuals of a colony. This would be associated with the appearance of alleles of sufficient activity (comp. p. 172).

Since, however, within many graptolite lineages, evolutionary changes occur through gradual spreading of corresponding characters, analogies of the genetic mechanism of these changes with those of penetrance and expressivity is very probable.

Genetic data indicate that changes in penetrance and expressivity may be influenced by genetic factors and definite environmental factors. The latter consist of temperature and trophic factors (Hadorn, 1955). These cannot be considered responsible for long-lasting and directional evolutionary changes ascertained in graptolites (comp. p. 199). Genetic factors are much more probable. Two of them have the greatest significance: 1) modifying genes altering the activity of phenotypic manifestation of definite genes, responsible for the appearance of certain features; 2) changes of the "major genes" themselves, responsible for individual morphological effects of directional character. Among them, the multiple alleles series, often resulting in directional phenotypic effects, should be placed foremost.

The significance of modifying genes for the activity of phenotypic manifestation of genetic factors has been shown in works of Timoféeff-Ressovsky (1931, 1934 and earlier), Hadorn & Gloor (1943, *vide* Hadorn, 1955) et alii. Experiments with the use of the artificial selection method clearly show how easily stocks may be produced, characterized by determined "genic balance", hence by determined expressivity and penetrance of a given gene. Moreover, changes in genic environment which determines the mode of phenotypic manifestation of a definite gene may result from the mutations of other genes. E. g. Morgan has shown that the "eyeless" mutation in *Drosophila*, expressed by reduction of eyes, will, after a sufficiently long line of generations, gradually revert to the normal state, i. e. its eyes will scarcely differ from those of the wild form. It has been ascertained that this is not a case of reverse mutation but of the mutation of other genes altering as modifiers the character of the genotype and affecting the phenotypic effect of the "eyeless" mutation (Šmalgauzen, 1946). Such functions may be carried out in the genotype by very diverse

genes changing the "genetic environment" (e. g. as shown by the investigations of Hersh (1929, *vide* Carter, 1951/1954) on manifestation of the "bar" mutation in *Drosophila*. The activity of phenotypic manifestation of a given character controlled by natural selection is determined and changed by way of corresponding selection of definite mutations. The picture presented by the history of numerous evolutionary trends of graptolites indicates beyond doubt that similar genetic mechanisms could have determined graptolite evolution too. It should then be recognized that when this supposition is taken into account, the growing expressivity of certain morphological characters are merely "Expressivitätstufen" (Hadorn, 1955) of the same basic gene whose individual phenotypic effect is intensified by the action of modifiers. This series of changes is well illustrated by the apertural processes in some Cucullograptinae, which represent the successive steps in the development of asymmetry (fig. 14 A, C, D). The thecae have been selected so that the basal width of metatheca is approximately the same, indicating that they occupied approximately the same position in the rhabdosome. The existing differences may be regarded as resulting from definite evolutionary changes and independent of astogenetic variation. Fig. 14 C, D show apertural processes differing in the degree of expression of the same features (hypertrophy and overlap of the left lobe, atrophy of the right lobe). They might be regarded as a result of changes in phenotypic expression of the same genetic factor or factors.

On the other hand, when considering changes of definite characters occurring over a sufficiently long period of time (evolutionary changes ascertained by Sudbury, 1958, within the *M. triangulatus* (Harkness) group; changes of astogeny described by Davies, 1929, in *Glyptograptus* cf. *persculptus* (Salter)), we may conclude that they involve not necessarily the intensity of phenotypic manifestation of one "basic allele" (oligogene) only, but a whole series of such alleles keeping to a definite direction of changes.

When considering the evolution of some simple morphological character (e.g. thecal shape or structure of apertural apparatus), we are referring to features which deserve to be called "unit characters" or "biocharacters" (as used by Swinnerton, 1932, 1947/1950). Modifications which affect such a character in the given lineage would justifiably be named "bioseries" (Swinnerton, 1947/1950) and would represent the successive evolutionary stages of a definite character whose morphological nature does not forbid it being determined by a single gene. Such changes, having a constant direction, and differing, indeed, merely in the degree of manifestation of the same features, may be regarded as

resulting from mutations bearing the character of multiple alleles. The latter are known often to form long series of mutations, whose individual members may successively produce one another. Their phenotypic effects are often distinguished by a regular increase or decrease of the activity of manifestation of certain characters.

Illustrations of such allelomorph series, representing a picture strikingly similar to the genetic changes probably occurring in graptolite colonies, are provided, among others, by the following series: the "vestigial" allelomorph series, to a various extent reducing the wings of *Drosophila*; the "white" mutation series changing eye colouration from a dark-red "wine" colouration to a completely white one; the "bar" mutation affecting the number of facets and the eye-shape, etc.

The "vestigial" allelomorph series (fig 18) is that particularly interesting and instructive in our case. It has been very thoroughly investigated by Mohr (1932) and interestingly interpreted by Goldschmidt (1938) and Carter (1951). A phenotype series of the particular mutations, constituting the allelomorphs of one gene, represents structures ranging from a nearly normal "nicked" wing to the short "no wing" rudiment. According to Carter, such mutations ought not really to be defined each as "different types of change in the gene, but as more or less extreme forms of the same change" (1954, p. 67). Multiple alleles series are just those frequently producing a picture of directional phenotypic effects and they may be relatively closely correlated with the character of evolutionary changes noted in graptolites. They show that "phenotypic effects of all members of the series are of the same general nature, varying only in the extent of their differences from the normal (non-mutated) type — varying, that is to say, only in the intensity of their action" (Carter, 1954, p. 65). In the case of certain multiple alleles series it has been ascertained that the gradual intensification of phenotypic effects is accompanied by correspondingly increased penetrance of that allele. Moreover, certain alleles series are regarded as an expression of changes in the amount of produced morphogenetic substances. i.e. they are referred to quantitative differences (Goldschmidt, 1938, for 'vestigial' series). This coincides quite well with the relations ascertained in graptolites.

On the base of fossil material only it is hardly possible critically to discuss the significance of either of the two just mentioned possibilities. Even though the picture provided by many of graptolite lineages strikingly resembles the phenotypic effects in multiple alleles series, still these analogies do not in the least prove similarities of the genetic mechanism of these processes. Generally speaking, changes in modifiers (multiple factors, i.e. polygenes) may with equal probability

be considered as responsible for these changes. We should, however, take into account investigations postulating that these factors do not by any means mutually exclude one another, but may combine, while differences between multiple alleles may have been intensified by corresponding modifiers. This may be inferred from works by Sirks (1926, 1931, *vide* 1956) on the heredity of quantitative characters in *Vicia Faba*. That author has ascertained that the varying shape of leaves in this plant is determined by 4 genetic factors, each of which produces a multiple alleles series. On the other hand, these factors produce two polymeric pairs whose phenotypic effects are mutually intensified (anisomeric polymery). It has been ascertained through the research work of Jenkins (1939, *vide* Schwanitz, 1954) on plant genus *Crepis* that taxonomic specific characters are based on a multiple alleles series. Hence they may constitute the basis of phylogenetic trends. In a number of other cases it has been proved that infraspecific heteromorphism consists of multiple alleles series.

At the present knowledge of this problem it is perhaps not too risky to advance as a working hypothesis the bold supposition that *in graptolites directional evolutionary changes consisted in orthoselection of modifiers changing the phenotypic manifestation of a definite "major gene" (oligogene) or in the selection of mutation forming series of multiple alleles*, each of them with distinct phenotypic effect, eventually modified by morphogenetic substances showing gradient along the rhabdosome. The choice of one out of the two alternatives is impossible on palaeontological evidence, but genetic data indicate that both these processes may have participated in evolution.

In view of the nearly complete lack of knowledge of the environment in which graptolites had lived, we are unable to determine the way of action of natural selection in their evolution nor the environmental factors of this evolution.

Since the time of Lapworth it is a common belief that Graptoloidea were epiplanktonic organisms who lived in open seas and oceans (comp. Ruedemann, 1934; Bulman, 1955, 1957 with References). On the whole, it is hardly to be expected that bottom sediments in which the graptolite remains are buried, could provide reliable information concerning the life conditions of Graptoloidea because they were deposited outside the biotope in which graptolites lived. Moreover, a number of cases distinctly suggests transport of graptolite remains and it may be consequently supposed that they had been buried in a different area than that in which they had lived (Bulman, 1955, 1957). With respect to graptolites, which are epiplanktonic organisms, we may reasonably

suppose that the distinct majority of fossil graptolite assemblages represent "subprimäre Lage" (Seitz & Gothan, 1928). This means that they had been transported "post mortem" and that probably a part of necrocoenoses constituted true tanatocoenoses (Davitašvili, 1945). This is indicated by the general lack of surfaces of the attachment and of the distal portions of the virgula, suggesting breaking off from the place of attachment and consequent transport by water currents. Similarly striking is the fact that graptolites cannot be associated with any definite sediment since they occur in almost every deposit (Bulman, 1955, 1957). All this evidence hardly permits a correlation between changes of sediments containing graptolites and changes of their abiotic environment. Only very large scale changes of the abiotic environment (change of facies, change of current relations) may be here sufficiently indicated and taken into account, such as e.g. those eventually responsible for a more or less general extinction of graptolite faunas (comp. Jaeger, 1959). Doubtlessly, changes in the abiotic environment had a decisive bearing on graptolite evolution, nevertheless data now available may permit to determine these connections in regard to changes of whole faunal complexes (migrations), but never in regard to evolutionary changes in definite phylogenetic lineages.

An analysis of faunal changes in graptolite facies shows that in graptolite evolution the directional evolutionary processes are not, as a rule, accompanied by distinctly directional changes of given sediments. The latter display a cyclic pattern and, sometimes, they long remain practically unchanged over extensive areas. Nevertheless, in such series, we note intense changes of the graptolite fauna even though considerable stability of the abiotic environment over large areas is apparently suggested by the nature of sediments.

Factors of evolution in particular graptolite lineages cannot be merely identified with any particular abiotic factor, but are doubtlessly to be expected in ecologic and selective mechanisms connected rather with biotic environment. The functional significance of changes in the shape of the rhabdosome and of thecae, however is not closely determined. One cannot adequately explain the physiological meaning of a number of observed changes and that hampers causal interpretation of graptolite evolution.

This explains why Bulman (1933) encountered such difficulties in determining the adaptive nature of graptolite evolution: "In such of the thecal elaboration trends as have been considered here, it has been suggested that they are not due to any direct environmental influence (which is, however, seen in local geographical variations in each series): and against the view that they are adaptive is the fact that at least

three types are initiated simultaneously, all under apparently the same condition of environment, and that regular regressive series also occur. Either they are not adaptive, or we must assume that the trends represent forms which did in fact live under slightly different conditions of environment (e.g. suspended in some way at different depths in the water and perhaps possessing some specialized feeding mechanism) for which view there is certainly no evidence. ...As concerns the graptolites, I offer the view that there is very little evidence that any of the trends originated in response to external conditions; they seem, on the contrary, far more readily referable to some internal factor" (Bulman, 1933, p. 332).

Some of the difficulties emphasized by Bulman (1933) have now to a certain extent been reduced.

An attempt is here made to illustrate this on example of evolution in the Cucullograptinae (comp. p. 176). This group was subject to intense differentiation bearing distinctly the character of an "adaptive radiation". Morphological differentiation is most strikingly expressed here in modifications of apertural apparatus of thecae. There seems to be little doubt that this differentiation was linked with adaptations to various feeding-mechanisms and each apertural apparatus was a kind of hydrodynamic tunnel which enabled better utilization of the food-supply available to microphages to whom graptolites most likely belonged (Urbanek, 1958).

This differentiation was realized in a time-span to which in deep-boring Mielnik, Eastern Poland, correspond deposits with total thickness approx. 90 m. In the lower parts they correspond to the *scanicus* zone (some 60 m) and in the upper part to 30 m thick series of sediments above this zone. These deposits consist of more or less regularly spaced intercalations of argillaceous shales and of marls or impure limestones each some 10—20 cm thick. This series represents, therefore, a good example of rhythmic sedimentation. Marly and limestone intercalations lithologically correspond well to Scandinavian erratic boulders containing the same fauna and there is no doubt that the latter were derived from analogous series, where most probably they formed corresponding horizons of concretions and lenses in graptolite shales. Such conditions must have been stabilized over extensive areas of the Upper Silurian sea in Ludlovian times. This may indicate that evolution of graptolites had occurred in the relatively stable conditions of abiotic environment, with only some cyclic changes in facies distribution. Evolutionary changes, therefore, cannot be considered as a mere response to the changing conditions of abiotic environment, but are evidently connected with the evolution of biocoenosis, with gradual occu-

pation of ecological niches of a given biotope, with further specialization of feeding-mechanism.

Palaeontological evidence indicates that some evolutionary processes are distinctly connected with changes of abiotic conditions (e.g. in the evolution of *Ostrea* — *Gryphaea* Joysey, 1959; *Turkostrea* — *Fatina* Gekker, 1953), while others occur in nearly constant abiotic conditions (e.g. faunal evolution within the Chalk Series of England, stressed by Bulman, 1933). Changes of the abiotic factors do not seem to be indispensable for every one of the evolutionary changes and most probably they were not directly connected with all the changes. Some processes were perhaps in the first place associated with changes of the biotic environment which may but do not have to occur at the background of changes in abiotic environment (distribution and ecology of seaweeds, changes in biocoenosis resulting from migration and evolution of other groups and allied evolutionary lineages). An analogy may be here drawn with certain North Sea associations of now living organisms. According to Schäfer (1957) they are characterized by biotically conditioned changes in faunal structure at stabilized abiotic conditions. Such relations may also have occurred in those cases of graptolite evolution which cannot be proved to be truly connected with the supposed changes of the abiotic environment.

The morphological character of modifications in Cucullograptinae suggests rather striking resemblance to the process of divergence observable in adaptation of some groups to different modes of life, biotopes and food supplies. This results in a picture rather similar to that of radiations in such groups as the well known Darwin's finches in Galapagos Islands; the Hawaiian honey-creepers; the fishes in African lakes.

In all these cases evolution is expressed primarily through modifications of the feeding apparatus and feeding habits.

In Cucullograptinae modifications concentrated on apertural apparatus leave no doubt that the latter factor was decisive. There seems little doubt that evolution of Cucullograptinae represent a good example of adaptation to particular ecologic niches in a common but intensively differentiated biotope. The differentiation of the biotope in a simplest way may be expressed by some stratification (as suggested by Bulman, 1933), which may be vertical or horizontal. It is known in the majority of marine biotopes (comp. Alle et alii, 1950), where nearly each species has its own zone of occurrence. Such stratification was encountered in recent sea-weeds, which may create in this way a number of independent ecologic niches of a biotope. Such a stratification, well marked in recent seas, was probably more sharply

stressed in ancient, palaeozoic seas due to lack of ecologic specializations in the particular sea-weed groups, each of them was adapted to rather strictly determined conditions of life (Zernov, 1949).

Common occurrence in the same assemblages of some species of Cucullograptine (e.g. *Lobograptus scanicus parascacicus* + *Cucullograptus pazdroi*; *L. scanicus scanicus* + *C. pazdroi*) indicates that they lived contemporaneously in the same biotope but must have probably occupied different ecologic niches, being an example of different direction of specilization. Some facts indicate, however, that *Cucullograptus hemiaversus* — *C. aversus aversus* — *C. aversus rostratus* represent successive stages of the same lineage and gradually are replacing each other in the course of evolution. This is confirmed by the fact that the presence of one of these forms excludes another from the known associations. Occurrence of some forms in the same fossil associations does not indicate that they really lived "side by side". E.g. since it is not excluded that some of them are secondary accumulations. Hence, in their life-time these forms may have occupied separate ecological niches though their remains were subsequently secondarily accumulated. These facts would account for the contemporaneous occurrence within the same association of forms representing various evolutionary trends.

The evolution of Cucullograptinae is fully understandable on the ground of the natural selection theory. Diferentiation of a common ancestral group seems to be an effect of fractionating selection (Simpson, 1953); some directional trends are most probably due to orthoselection. The action of selection in the latter case must have occurred according to a similar pattern as that in the experiments of Timoféeff-Ressovsky (1934) and of Hadorn & Gloor (1943, *vide* Hadorn, 1955). These indicate that through artificial selection some genetic stocks may be easily obtained, with stabilized system of modifiers, or "major genes" with a definite activity.

The apparently paradox fact of the simultaneous progressive and regressive development within definite genetic trends of representatives belonging to the same association may be also accounted for by other genetic phenomena. It is, indeed, frequently encountered that the behaviour of some genetic factors varies in related species. In some it merely causes normal morphological phenomena, while in others it leads even to hypertely and hypertrophy, or is manifested as a semi-lethal or lethal factor (frequently discussed experiments on the manifestation of the same allele in various species of cotton (*Gossypium*), e.g. Harland, 1936; Šmalgauzen, 1946; Wagner & Mitchell, 1955; manifestation of the "migra" gene responsible for pigmentation in various genera

of small fishes *Platyopocilus* and *Xiphophorus*, causing normal pigmentation in the former and tumors and hypertely of tissues in the latter; Harland, 1936; Dodson, 1952; heterosis etc.).

Differences in genomes and corresponding differences in "genic balance" within various graptolite lineages may have been responsible for the adaptivity of certain factors in one case, while in another their phenotypic expressivity was extinguished by genetic selection since they proved to be inadapative (phenomena analogous to the action of suppressors controlling the development of a "normal" phenotype in spite of the presence of mutations controlling the occurrence of a new mutant phenotype; Šmalgauzen, 1946, Wagner & Mitchell, 1955). These may be the reasons determining e.g. the progressive development of rastritiform thecae within the evolutionary trend *M. triangulatus triangulatus* (Harkness) — *Rastrites longispinus* (Perner), while within the line *M. triangulatus separatus* Sudbury — *M. triangulatus fimbriatus* (Nicholson) they are, according to Sudbury (1958), subjected to secondary regression. The phenotypic manifestation of a mutation controlling the rastritiform structure of thecae has been here "extinguished" by other genes or a whole assemblage of genes.

Thus, certain processes in graptolite evolution, at first sight not immediately understood from the viewpoint of the genetic theory of natural selection, may be explained by previously recognized genetic mechanisms.

V. TAXONOMIC CONSEQUENCES

The acceptance of a definite viewpoint concerning the mode of evolutionary changes in graptolite colonies permits us in a different light to consider some problems pertaining to their systematics.

The examples discussed here above seem to prove that in a number of graptolite evolutionary trends structural changes of thecae occur gradually and the extreme morphological types may be united by a line of intergrading forms, which differ quantitatively only. These cases clearly indicate that originally uniform forms may, in result of modifications affecting a part of thecae, become "biform" forms. These, in turn, after complete penetrance of the new thecal type, will secondarily become uniform. Numerous examples of such processes have been illustrated in the works of Bulman (1933, 1951) and Sudbury (1958) moreover, they may be inferred from the research work by Davies (1926) and that of the present writer in respect to the previously cited examples of Cucullograptinae and Saetograptinae.

These studies reasonably suggest that on the whole "biform" forms are a transient intermediate stage of evolution, leading to secondary uniformism of thecae. In most cases this is the apparent condition. Exceptions from this rule, however, are encountered, showing the stabilized nature of some biform forms which do not lead to the formation of secondarily uniform forms. Bulman (1951, p. 326-7) gives an example of this kind when he writes that *M. decipiens* Törnquist "seems to represent a relatively stable condition of half-developed *Rastrites* (like the relation of *Sub-Holostei* to *Holostei* among fishes)". Most probably we are dealing here with differences in the rate of evolution in various evolutionary lines. Some of the progressive lines relatively quickly attained secondary uniformism, others more slowly, while certain of them have been arrested at a definite evolutionary stage. Moreover, Sudbury (1958) cites examples of the "reversibility" in evolution of certain thecal characters. They concern graptolites provided with rastritiform proximal thecae which are lost during later evolution (*Monograptus triangulatus separatus* Sudbury — *Monograptus triangulatus fimbriatus* (Nicholson)). All these data confirming that uniform types may originate from biform types, and the other way about, contribute to make still more intricate the picture of graptolite evolution.

One of the first problems here is that of the significance and importance of the establishment of taxonomic units (genera) differing from related forms in strongly expressed biformism and characterized by the occurrence of thecae encountered in other genera. As examples of such genera one may mention here *Diplograptus* McCoy (Diplograptidae), also *Pernerograptus* Přibyl and *Demirastrites* Eisel (Monograptidae)³². From a strictly morphological viewpoint these genera are a transition between two other genera in which fundamentally the same type of thecae occurs on the whole length of the rhabdosome. *Diplograptus* e.g. intergrades between *Amplexograptus* Elles & Wood (proximal thecae) and *Orthograptus* Lapworth (distal thecae); *Pernerograptus* unites the characters of *Monograptus* Geinitz (proximal thecae) and those of *Pristiograptus* Jaekel (distal thecae), while *Demirastrites* is a transient form intermediate between *Rastrites* Barrande (proximal thecae) and *Monograptus* Geinitz (distal thecae).

The position of *Diplograptus* is the most uncertain one and we do not know whether forms here referred are actually intermediary links

³² Genera *Colonograptus* Přibyl and *Saetograptus* Přibyl, differing in the extent of biformism, are not discussed here since their main diagnostic character is not the degree of biformism but structural differences of apertural processes (Přibyl, 1942; Urbanek, 1958).

between those with amplexograptid or orthograptid thecae on the whole length of the rhabdosome. Discontinuous stratigraphic distribution (break in the Upper Ordovician!) apparently suggests that this either is a heterogeneous group probably representing an analogous stage in the evolution of various diplograptid lineages, or else partly an assemblage of these forms distinguished by stabilized biformism.

The position of the genus *Pernerograptus* Přibyl seems to be somewhat more clearer. It has been demonstrated in the case of at least some forms here referred (genoholotype: *Monograptus argenteus* (Nicholson)) that they are indeed links of an evolutionary chain, distinguished by gradual spreading of "hooked" thecae. Hence, the attainment during this evolution of a stage with this thecal type on the whole rhabdosome length seems quite probable³³ (data of Bulman, 1951, and particularly of Sudbury, 1958). In this meaning at least a part of the forms here referred are transient between those referred to *Pristiograptus* Jaekel and *Monograptus* Geinitz. Next to them is probably grouped a certain number of forms branching from the main stock, which need not necessarily have led to "secondary uniformism".

In many respects similar changes in the structure of apertural apparatus must have occurred in different lineages leading to formation of similar but not necessarily homologous structures. This is confirmed by the presence in the Lower Ludlovian of some forms (*Monoclimacis micropoma* (Jaekel)) with apertural lobes not representing the prolongation of interthecal septum of their own metatheca and with peculiar microstructure and therefore unhomologous to apertural lobes in *Monograptus* (*Monograptus*), (Urbanek, 1958). Similar conclusions are suggested by the interesting data of Jaeger (1959) concerning the geologically youngest monograptids (ey-beds). According to Jaeger, the gradual spreading of apertural lobes — from the proximal toward the distal part of rhabdosome — has taken place in two lineages distinguished by him (comp. p. 139). In result of such changes the apertural apparatus has acquired a "hooked" appearance and is even termed by Jaeger as the "uncinatus type" of thecae. According to Jaeger, apertural lobes in these forms (*M. hercynicus* Perner, *M. uniformis* Přibyl, *M. praehercynicus* Jaeger) are formed when building of the next theca has just only started, therefore, as in typical *Monograptus* (*Monograptus*). Whether they correspond fully to apertural lobes of the latter genus remains, however, somewhat uncertain. Jaeger's figure (1959, fig 16 f) seems to clearly indicate that in distal thecae of *M. uniformis* apertural lobes cannot be considered as direct prolongation of interthecal septum. Also the regular

³³ The connection of *argenteus* series (*Pernerograptus*) with the *prionon* one (*Monograptus*) is, however, to some extent uncertain (Bulman, 1951).

size decrease of lobes distally, noted in forms described by Jaeger, is not known in true *Monograptus* (*Monograptus*). Some analogy, however, may exist between modifications observed in Jaeger's monograptids and processes of the gradual spreading of "hooked" thecae in *Pernerograptus*, without any clear evidence that in both cases apertural apparatus are really homologous.

The genus *Demirastrites* Eisel is by some students regarded as a group independent of *Rastrites* Barrande. Its evolution is claimed to be parallel to that of *Rastrites* Barrande but not constituting an evolutionary transition from *Monograptus* Geinitz to *Rastrites* (Příbyl & Münch, 1941). This opinion has been weakened by the investigations of Bulman (1933, 1951) and still more so by those of Sudbury (1958) proving the existence of direct connection of the "triangulate monograptids" (group of *M. triangulatus* (Harkness)) as the genolectotype of *Demirastrites* Eisel (Příbyl & Münch, 1941) and the typical representatives of *Rastrites* Barrande. With regard to some forms assigned to *Demirastrites*, such as *M. decipiens* Törnquist, it is probable that they were not a transition to rastritiform forms, but represented stabilized biform types (Bulman, 1951).

On the whole, however, both *Pernerograptus* Příbyl and *Demirastrites* Eisel may be regarded as grouping various species, some of which were probably true transitions between the two genera. They represent a definite evolutionary stage, on the whole adequately reflecting the course of evolutionary events. It is, however, quite doubtless, that they are an assemblage of different evolutionary lineages and that, as morphological groups representing a defined stage of evolution, they are intersected by them. The same is, however, applicable to uniform forms which likewise are groups representing only a definite morphologic stage of evolution and, moreover, heterogeneous assemblages of species. The tendency to base systematics on true evolutionary lineages seems to be unrealistic owing to the intricacy of that evolutionary picture and the predominance of the hypothetical element in the determination of these lineages. Hence morphological groups, only partly natural, used as the base for systematics, seem to be a necessary concession. The fact, however, that groups established on biformism of thecae may, at least partly, be regarded as transitions, arouses numerous doubts as to whether we should attempt to separate them, or — on the contrary — to include them into their ascendant or descendant genera.

The reasons against the separation of such forms are as follows: a) that they are morphologically transient forms, b) that they are heterogeneous assemblages consisting of a certain number of phylogenetic lineages.

Reasons supporting the separation of such forms are: a) they are not all transient forms, at least some of them had displayed a stabilized

biformism, b) groups of uniform graptolites are heterogenic too, while some of the biform genera represent a definite stage in the evolution of certain lineages and, on the whole, provide reliable information as to its direction (*Pernerograptus*, *Demirastrites*).

Should we think justifiable the establishment of such biform genera as *Pernerograptus* and *Demirastrites*, we must keep in mind that other genera will unite both biform and uniform forms (e.g. *Cucullograptus*). The separation of biform genera would be reasonable only when they involve sufficiently numerous groups (a score or so of species and varieties referable to several evolutionary lineages and representing an important trend in evolution). When, however, these forms are numerically restricted and representing probably a small number of separated evolutionary lineages only, the separation of biform forms from the uniform would hardly be reasonable.

In the light of these considerations the recognition of biformism as reliable ground for generic distinction in monograptids is hotly disputed and open to further discussions. In order not to anticipate its solution the writer does not use here respective generic names. He believes that besides its fundamental significance this problem has its conventional aspect which ought to decide as to which alternative should be accepted in formal taxonomy³⁴.

Generally speaking, however, the writer believes there is sufficient ground for the separation of such biform genera as *Pernerograptus* Přibyl and *Demirastrites* Eisel, though their separation into distinct subfamilies (Přibyl, 1946) does not seem reasonably justified. The following is a comparative table of similarities between the supposed hypothetical ancestors, the intermediate forms represented by these genera and their hypothetical descendants.

1. Uniform forms with straight thecae on the whole rhabdosome length — <i>Pristiograptus</i>	→	Biform forms with hooked proximal thecae and straight distal thecae — <i>Pernerograptus</i>	→	Uniform forms with hooked thecae on the whole rhabdosome — <i>Monograptus</i> s.s.
2. Uniform forms with triangulate hooked thecae on the whole rhabdosome length — <i>Monograptus</i> s.s.	→	Biform forms with rastritiform proximal thecae and triangulate hooked distal thecae — <i>Demirastrites</i>	→	Uniform forms with rastritiform thecae on the whole rhabdosome length — <i>Rastrites</i>

³⁴ The latter aspect is closely linked with the general problem of taxonomy of genus *Monograptus* s.l. The writer is convinced that the division of this genus into several independent genera is by all means a sound concept, but the realization of the division is a matter for discussion and appropriate convention.

It follows that differences between originally uniform forms (ancestors of biform forms) and their biform descendants are morphologically speaking more substantial (appearance of a new character absent in the ancestors), than those between the biform forms and forms secondarily uniform (descendants of biform forms differing from them in the quantitative spreading of a character previously present in ancestors). Forms such as *Pernerograptus* in this respect come closer to the genus *Monograptus* — since differences between them seem to be quantitative (degree of manifestation of the same character) — than to the genus *Pristiograptus* (presence or absence of a given character). Hence it would seem more reasonable to assign them to the subfamily Monograptinae than to separate them, after Přebyl (1946), into an independent subfamily, the Pernerograptinae. Correspondingly it would perhaps be more correct to refer the genus *Demirastrites* Eisel to the subfamily Rastritinae than to separate it into the subfamily of Demirastritinae (Přebyl, 1946). This proposition is suggested by the boundary between ancestors of these genera being more pronounced than between them and their descendants where it is less sharp and rather quantitative.

The problem of the taxonomic significance of proximal and distal thecae is associated with the here discussed questions. Elles and Wood (1901-1918) based their division of monograptids into groups of species rather on the structure of "mature thecae". Subsequently, however, Elles (1922) arrived at the conclusion that proximal thecae are of particular significance in the evolution of that group (comp. p. 138). When going into that problem Sudbury (1958) and Urbanek (1958) independently drew the conclusion that in monograptids proximal thecae are of greater practical significance, though the distal ones may, obviously, have some definite significance too. In the light of new data this conclusion requires to be supplemented since in certain groups (Cucullograptinae, Cyrtograptinae?) it may well be reversed. Taking into account now available data, the following would be a reasonable conclusion: evolutionary changes in graptolite colonies (particularly so in monograptids) are initially manifested at one end of the colony only, hence thecal structure in that end is of foremost importance in explaining the direction of evolution and the nature of the occurring modifications, as these anticipate further evolution. Thecae in the opposite end of the colony, whose structure remains approximately unchanged, provide information regarding the structure of ancestors. Since, however, thecae may be "introduced proximally or distally" in the particular lineages, either the proximal or the distal thecae may adequately supply the necessary evidence. The appearance of new characters, absent in ancestors, is the base for establishing minor taxonomic units; hence greater significance

should be assigned to thecae in which these changes are manifested primarily. Since in the majority of cases they are manifested in the proximal end, the attention of the taxonomist is most frequently focused on them, though this cannot be accepted to be the rule. The most appropriate method will doubtlessly be correctly to interpret the structure of both the proximal and the distal thecae and to compare their structure with that in other related forms.

VI. CONCLUSIONS

In many Graptoloidea thecae display a regular morphologic succession along the rhabdosome. It is manifested by gradual modifications of thecal structure, consisting either in the presence or absence of the corresponding thecal segment, as well as in various structural modifications of the same thecal segment. After analysing these astogenetic modifications we are led to suppose that they express corresponding morphophysiological gradients. In agreement therewith colonies of Graptoloidea display a certain polarity in their organization pattern. This was most likely determined by the mode of the formation and distribution of certain morphogenetic substances which had a decisive bearing on the structure of the successive zooids. These substances, supposedly produced by the siculozoid, would spread along the rhabdosome, showing a definite gradient. The siculozoid would probably be here a centre of physiological dominance over the remaining individuals of the colony. This working hypothesis is applicable to both, the uniaxiate and the multiaxiate colonies. The main stipe and the successive lateral branches (cladia) in *Cyrtograptus* may be regarded as centres of dominance of higher orders which control in turn the rate of budding and the morphological succession on the next branches.

As has been ascertained in a number of lineages of Graptoloidea, their evolution consists in the gradual spreading of the new thecal type which at first is introduced either proximally or distally into the rhabdosome. Since a graptolite colony is a kind of clone, the morphological differences between the individuals of a colony express only the various phenotypic manifestation of the same genome. Graptolite evolution would consist in modifications of astogeny, and these modifications would, therefore, express only the varying degree of penetrance and of the expressivity of the particular genetic factors within the colony. These changes would be probably caused by mutations of genes controlling the development of definite thecal characters, or altering the amount of morphogenetic substances produced by the siculozoid. Genetically, the

latter act as stimulators or inhibitors of the phenotypic manifestation of definite genetic factors, i.e. they behave as if dependent on definite modifiers. When in ancestors new characters are at first introduced distally only, later spreading over the proximal part, we must accept that modifiers control the production by the siculozoid of the morphogenetic substance which acts as an inhibitor of these characters. During phylogeny, in result of successive mutations, the activity of genes responsible for the development of a definite character would increase, or the activity of the inhibitor would decrease. When, on the contrary, in ancestors the new character is at first introduced proximally only, later to spread distally too, we must accept that modifiers, and at the same time the substance produced by siculozoid, behave like stimulators of the given character. The activity of genes determining a given character or that of the stimulator would increase during the evolution of such forms. An analysis of evolutionary changes within some phylogenetic lineages ascertains that they affect a definite complex of characters and retain a definite direction. Hence, they behave similarly as 1) cumulative factors (modifiers), or as 2) multiple alleles constituting series of alleles with directional effect of phenotypic manifestation and with varying activity. Thus the general genetic mechanism of changes in graptolite colonies would consist in the occurrence of mutations, in which the phenotypic manifestation of alleles was first low, while later the penetrance and expressivity gradually increase.

The present work, moreover, contains discussions on the taxonomic consequences of the new concept regarding the organization of graptolite colonies and the probable genetic mechanisms of their evolutionary changes.

APPENDIX

DESCRIPTION OF NEW SPECIES AND SUBSPECIES CITED IN THE TEXT³⁵

Family **Monograptidae** Lapworth, 1873
 Subfamily **Cucullograptinae** Urbanek, 1958
Lobograptus Urbanek, 1958
Lobograptus simplex n. sp.
 (pl. I, fig. 1 a-c; text-fig. 13 A, 14 A, 19, 20)

Holotypus: pl. I, fig. 1 a-c, medial part of rhabdosome.

Paratypus: fig. 19 A₁-A₂, single distal transparent theca.

Derivatio nominis: *simplex* — Lat. simple, uncomplicated.

Diagnosis. — Cucullograptid with straight sicula provided with well developed dorsal process; proximal thecae thin, tubular, slightly overlapping, with straight ventral walls and probably a dorsal curvature; distal thecae distinctly expanded in metathecal portion, with distinctly sigmoidal ventral wall and notable overlap; thecal apertures throughout the rhabdosome length provided by two symmetric lateral apertural lobes which do not touch above the aperture.

Material. — Several dozens of short, mostly unflattened rhabdosome fragments; the longest one with 7 thecae. Several siculae with the 1st theca. State of preservation adequate for reconstruction of astogeny.

Description. — Sicula 1.52—1.40 mm in length including the dorsal process (without it 1.48-1.36 mm), terminating below the aperture of 1st theca (fig. 13 A). Dorsal process of metasacula distinct. First theca length of 1.56-1.76 mm. Proximal thecae thin, tubular, 1.72-1.76 mm in length, prothecae 1.40-1.48 mm in length, 0.12 mm in breadth, metathecae 0.28-0.32 mm in length (the apertural apparatus included), maximum breadth of metathecae 0.20 mm. Distance between apertures of adjacent thecae about 1.50 mm. Slight bending of proximal fragments of rhabdosome suggests the presence of its dorsal curvature. Distal thecae distinguished by notably sigmoidal curvature of the ventral

³⁵ These species will be more at length described in a paper by the present writer, now under preparation, on the morphology and evolution of the Cucullograptinae group.

wall — breadth of protheca 0.20-0.28 mm, maximum breadth of meta-theca 0.44-0.52 mm. Length of distal thecae 2.08-2.28 mm, length of protheca 1.56-1.72 mm, length of meta-theca 0.52-0.60 mm. Distance between adjacent apertures of distal thecae 1.52-1.68 mm. Nearly 7 thecae fit into 10 mm of the medial part of the rhabdosome.

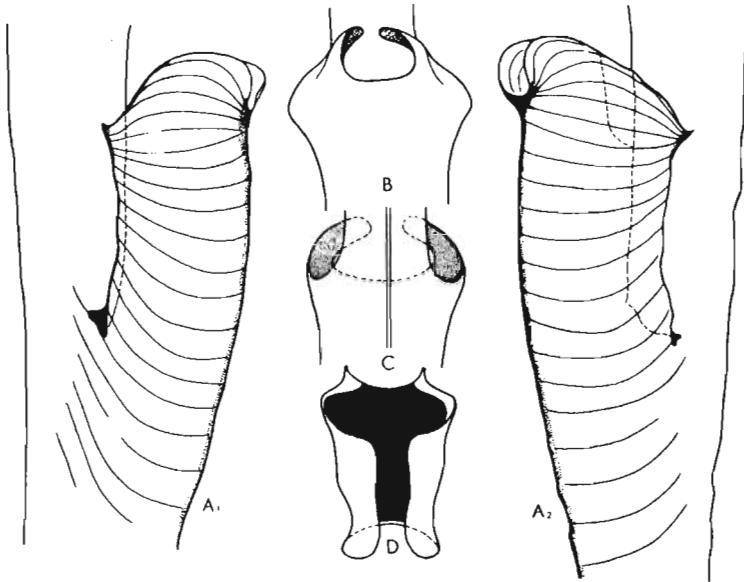


Fig. 19. — Structure of thecae in *Lobograptus simplex* n.sp. A fusellar structure of distal theca: 1 right side view, 2 left side view; B apertural part of distal theca, ventral view; C apertural part of distal theca, dorsal view; D apertural part of distal theca, top view (boulder S. 219, Lublin), approx. $\times 70$.

Thecal apertures provided with two distinctly symmetric apertural lobes (fig. 19 A), overlapping the aperture (fig. 19 B, C) but not touching each other and fairly widely separated by a fissure (fig. 19 D). Lobes made up of few, arcuately bent fuselli (4 to 7), some of which (1 to 4) thin out dorsally without reaching the thecal wall, and giving the processes the shape of triangular ears (fig. 20). Fusellar structure of lobes strikingly resembles that of apertural lobes in *Lobograptus exspectatus* n.sp. and of *L. scanicus parascanicus* (Kühne), (fig. 20).

Occurrence. — "In situ" not recorded. Etched from a Silurian erratic boulder, of Scandinavian origin, S. 219, collected at Lubin in the island of Wolin, Western Pomerania. The associated graptolite assemblage consists of *Pristiograptus dubius* (Suess), and *Monoclimacis* cf. *micropoma micropoma* (Jaekel). This assemblage does not reliably indicate the exact stratigraphic horizon from which the collected boulder is derived,

but the presence of *M. cf. micropoma* suggests the *scanicus* zone. Most probably it is the lower part of that zone or the upper part of the *nilssoni* zone.

Systematic position. — The symmetry of apertural lobes and their slight development justifies the view that *L. simplex* n.sp. may have led to *L. exspectatus* n.sp. and, by way of further development of the apertural lobes and the introduction of asymmetry, also to the remaining Cucullograptinae. Thecal structure and the supposed presence of dorsal curvature in the proximal part of the rhabdosome apparently suggest that *L. simplex* n.sp. is linked with other forms from erratic boulders, displaying simpler structure of apertural lobes. This may possibly suggest that Cucullograptinae descend from forms with simple pristiograptid thecae, and not, as has been heretofore believed, from those with the hooked type of apertural lobes (comp. Urbanek, 1958, p. 23).

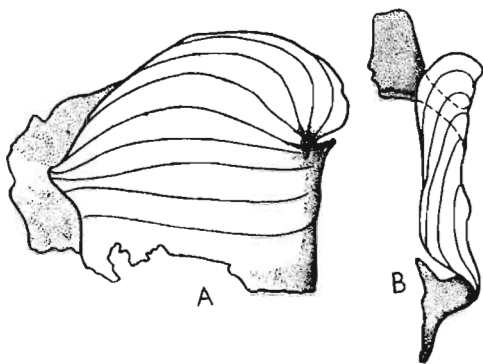


Fig. 20. — Fusellar structure of apertural lobe in *Lobograptus simplex* n.sp., illustrated by isolated and transparent right lobe: A side view, B top view (boulder S. 219, Lubin); approx. $\times 105$.

Lobograptus exspectatus n.sp.

(pl. II, fig. 1 a-b, 3, 4; text-fig. 13 B, 14 B)

Holotypus: pl. II, fig. 1 a-b, rhabdosome fragment, probably a nearly distal part.

Derivatio nominis: *exspectatus* — Lat. expected.

Diagnosis. — Cucullograptid with straight sicula, provided with a moderately marked dorsal process; proximal thecae tubular, thin, with very small overlap; distal thecae in metathecal portion expanded and provided with gently sigmoidal curvature of the ventral wall and with distinct overlap; thecal apertures on the whole rhabdosome length provided with two symmetric lateral apertural lobes overlapping the aperture and medially touching one another.

Material. — Some dozens of short rhabdosome fragments, the longest one with 7 thecae, several siculae with the 1st theca. Well enough preserved for reconstruction of astogeny.

Description. — Sicula about 1.40 mm long, terminating at the level of 1st theca. Apertures of proximal thecae spaced approx. 1.04 mm.

Breadth of protheca in these thecae about 0.08-0.12 mm, breadth of metatheca 0.20 mm. Apertures of distal thecae spaced about 0.96-1.44 mm. Breadth of protheca here approx. 0.28 mm, that of metatheca about 0.44-0.64 mm. Approx. 7 thecae fit into 10 mm of the distal part of the rhabdosome.

Thecal apertures provided with two lateral apertural lobes (fig. 14 B), seemingly downhanging, overlapping the aperture (pl. II, fig. 3 a-b). The lobes form a sort of roof over the aperture. Antero-ventral margin of lobes bluntly terminated, nearly straight. Median margins of lobes may slightly overlap, the right lobe being sometimes overlapped by the left or the other way about. This seems an at random arrangement. Hence there is no definite asymmetry noted in the lobes either with regard to overlap or size, and practically speaking, they are symmetric throughout the rhabdosome. The fusellar structure of lobes strongly resembles that of apertural lobes in *Lobograptus simplex* n.sp. and *L. scanicus parascanicus* (Kühne), (pl. II, fig. 4). The lobe here is made up of arcuately bent fuselli, gradually shortening, so that the last ones thin out dorsally, at about the middle of the lobe.

Certain bendings of the proximal fragments seem to suggest a slight ventral curvature of the rhabdosome.

Occurrence. — Thus far unknown "in situ". Etched out of a Silurian erratic boulder of Scandinavian origin, S. 210, collected on the sea-beach at Ustka, Western Pomerania. The accompanying graptolite assemblage consists of *Pristiograptus dubius* (Suess), *Saetograptus chimaera* cf. *cervicornis* Urbanek, *Monoclimacis micropoma nannopoma* (Jaeger) and some few specimens of *Monoclimacis haupti* (Kühne). Two (?) other new species have, moreover, been ascertained.

The composition of this assemblage suggests that the boulder is most likely referable to the lower part of the *scanicus* zone, but neither is the uppermost part of the *nilssonii* zone to be excluded.

Systematic position. — In the fusellar structure of apertural lobes this form approaches nearer to the genus *Lobograptus* Urbanek than to *Cucullograptus* Urbanek. Typical representatives of the former genus (*L. scanicus scanicus* (Tullb.) and *L. scanicus parascanicus* (Kühne)) differ, however, in more straight arrangement of lobes and their asymmetry. From *L. simplex* this species differs above all in further development of lobes, touching over the aperture.

Most probably, the form described by the writer (Urbanek, 1958, fig. 43-44, p. 74-76) incorrectly as *Lobograptus parascanicus* (Kühne) is conspecific with *Lobograptus expectatus* n.sp.

Cucullograptus Urbanek, 1954*Cucullograptus hemiaversus* n. sp.

(pl. II, fig. 2 a-b; text-fig. 2 A, 6, 13 E, 14 C)

Holotypus: pl. II, fig. 2 a-b, a fragment of the nearly distal part of the rhabdosome.

Derivatio nominis: *hemi* — Lat. half; *aversus* — Lat. turned. Extent of overlap of the left lobe smaller than in *Cucullograptus aversus* (Eisenack).

Diagnosis. — *Cucullograptid* with straight sicula, nearly lacking the dorsal process; proximal thecae thin, tubular, hardly overlapping, distal thecae notably broader, in the metathecal portion with a distinct sigmoidal curvature of the ventral wall and strongly overlapping; thecae provided with two apertural lobes, proximally nearly symmetric, in the medial thecae the left lobe characterized by hypertrophy and a progressive overlap of the right lobe, in distal thecae it overlaps two thirds of the right lobe margin which is partly reduced.

Material. — A score or so of simple thecae and rhabdosome fragments, two siculae without the first theca. Reconstruction of astogeny possible.

Description. — Sicula about 1 mm long, probably terminating below first theca (fig. 13 E). Length of proximal thecae over 1.60 mm, probably up to 2.40 mm. Breadth of protheca here approx. 0.08 mm, that of metatheca 0.20 mm, length of metatheca about 0.08–0.12 mm. Length of distal thecae approx. 2.12 mm, breadth of protheca here 0.20 mm, that of metatheca about 0.36 mm, length of metatheca approx. 0.80 mm.

Right lobe made up of arcuately bent fuselli, flattened; left lobe with similar fusellar structure gently domed, provided with a small beak. In medial and distal thecae the convexity of the left lobe increases similarly as its overlap onto the right lobe (fig. 6). By folding the margin the right lobe forms an incision in the antero-ventral portion to accommodate the expanding left lobe. Fusellar structure and shape of the left lobe (fig. 6) conspicuously analogous to the structure of that lobe in *Cucullograptus aversus rostratus* n. subsp.

Occurrence. — "In situ" unknown. Etched out of a Silurian erratic block, of Scandinavian origin, S. 200, collected on the sea-beach in Rewal, Western Pomerania. The accompanying graptolite assemblage contains *Pristiograptus dubius* (Suess), *Saetograptus chimaera* cf. *salweyi* (Hopk.) and *S. chimaera* cf. *cervicornis* (Urb.). Most likely this erratic block was derived from the upper part of the *scanicus* zone. Similar forms (*C. cf. hemiaversus*) have been found in deep-boring Mielnik (ccmp. p. 180).

Systematic position. — Structure of thecae, most particularly that

of apertural lobes, leaves no doubt that this species belongs to the same evolutionary trend as *Cucullograptus aversus* (Eisenack), but that it represents a lower morphological stage expressed only in partial reduction of the right lobe and smaller hypertrophy and overlap of the left lobe.

Cucullograptus aversus rostratus n. subsp.

(pl. III, fig. 1-5; text-fig. 13 G, 14 D, 21)

1954. *Monograptus aversus* Eisenack; A. Urbanek, Observations on some Monograptidae, p. 297-300, fig. 9-12.

1958. *Cucullograptus aversus* (Eisenack); A. Urbanek, Monograptidae from erratic boulders, p. 70-72, fig. 36-39.

Holotypus: pl. III, fig. 5, single distal theca.

Paratypus: pl. III, fig. 3, single medial theca.

Derivatio nominis: *rostrum* — Lat. beak; provided with a beak-shaped process of the left lobe in more distal thecae.

Diagnosis. — From the typical form, *Cucullograptus aversus aversus* (Eisenack), (Eisenack, 1942, pl. 2, fig. 1-10; also pl. II, fig. 6 of the present paper), it differs in doming of the left lobe, stronger folding of its free margin, and in the presence of a well developed spade-like outgrowth forming a distinct beak on left lobe; in the distal thecae this outgrowth attains a length equal to that of the left lobe, in medial thecae it is smaller, in proximal lacking. These differences are distinct enough to permit the separation of that form into a new subspecies.

Material. — Simple thecae from erratic boulders and very numerous fragments, including siculae from bore-core Mielnik. Reconstruction of astogeny possible.

Description. — Thecae on the whole resembling those of *Cucullograptus aversus aversus* (Eisenack); sicula straight, tubular, 1.00-0.80 mm long, provided with a very poorly developed dorsal process. Proximal thecae thin, tubular, 2.00-2.12 mm in length, length of protheca 1.96-1.84 mm, that of metatheca including the apertural lobe 0.16 mm. width of protheca 0.06-0.12 mm, that of metatheca 0.12-0.16 mm. The most distal ones among the known thecae are provided with a strongly expanding metatheca, but are without a distinct curvature of the ventral wall. Length of more distal thecae 1.80-2.20 mm, length of protheca here 1.80-1.44 mm; length of metatheca including the lobe 0.36 to 0.40 mm, breadth of protheca 0.12 mm, maximum breadth of metatheca 0.20-0.24 mm³⁶. There are 7 thecae in 10 mm of the medial part of the rhabdosome.

³⁶ Measurement data based on the better preserved specimens from a core from the Mielnik boring.

Apertural apparatus composed of the left lobe only which displays hypertrophy and overlaps the aperture. Right lobe vestigial, represented merely by a narrow and folded apertural lip, covered by the left lobe (fig. 21, broken lines). Left lobe of median and distal thecae provided with a terminal outgrowth either in the shape of a short spade (boulder S. 121, comp. pl. III, fig. 1,2), or somewhat longer and sharply pointed (boulder S. 205, comp. pl. III, fig. 3-5; also specimens from the bore-core of the Mielnik boring). This outgrowth may be either nearly straight or sinistro-dorsally bent with a tendency to slight spiral coiling. The size of the outgrowth increases successively in the distal direction (fig. 21 C), while the most proximal thecae are without it, but provided with additional membrane on ventral wall (fig. 21, A, B, m).

Remark. — The writer's specimens (1954, 1958) strongly resemble forms described by Kühne (1955, fig. 13, p. 389-391), which seem reasonably referable to the subspecies *rostratus*, even though their outgrowth on the left lobe is slightly less well developed than that in typical forms.

Occurrence. — Thus far known from numerous rhabdosome fragments and single thecae. In the writer's material known from Silurian

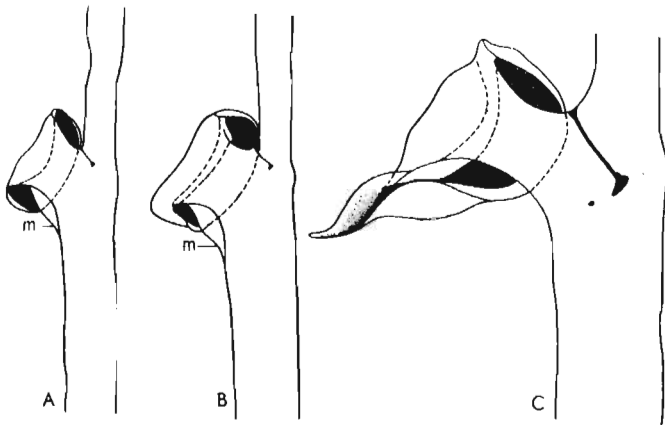


Fig. 21. — Astogenetic variation of thecae in *Cucullograptus uversus rostratus* n. subsp. A first theca, B medial theca, C more distal theca, all left side view; m additional membrane on ventral wall (deep-boring Mielnik, depth 925 m); approx. $\times 70$.

erratic blocks of Scandinavian origin, S. 121 and S. 205, collected at sea-beaches at Jarosławiec and Ustka, Western Pomerania. In the first of the named boulders this form is not accompanied by any other graptolite fossils, while in S. 205 it occurs in an assemblage containing *Pristiograptus dubius* (Suess) and some badly preserved forms, possibly

referable to *Monoclimacis* cf. *haupti* (Kühne). Quite recently it has also been discovered in a bore-core (deep boring at Mielnik on the Bug, at depth between 920 and 925 m). It occurs there in association with *Pristiograptus dubius* (Suess) and *P. bohemicus* (Barr.), also *Scolecodonta*. The presence of this form is characteristic of a layer occurring 9 m above a bed with *M.* cf. *leitwardinensis* (Hopkinson), some 15 m above the latest occurrence of *Saetograptus chimaera* cf. *salweyi* (Hopkinson) and 30-35 m above the true *scanicus* zone. This suggests the upper part of the Lower Ludlovian as the probable "stratum typicum" or, in any case, horizons distinctly higher than the top of the *scanicus* zone.

Systematic position. — Doubtlessly this form is very closely allied with *Cucullograptus aversus aversus* (Eisenack), (pl. II, fig. 6) from which it differs, however, in stronger expressivity of a number of characters and more advanced development of the apertural apparatus. Hence it may be considered as a more advanced evolutionary stage of the same phylogenetic lineage.

* *
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The name *Lobograptus scanicus scanicus* (Tullberg) is here applied to a form identical with that described by Bulman (1953) as *Monograptus scanicus* Tullberg. The relation of that form to Tullberg's originals (type specimens) described from Scania (Cardiolaskiffern, Marianelund; Skånes graptoliter, II, 1883, pl. 2, fig. 38-44) have not, however, been as yet determined. These specimens were not accessible to the writer, and probably were lost, while the Ask specimens, by Tullberg identified as *M. scanicus*, which were made available through the courtesy of Dr F. Brotzen from Sveriges Geologiska Undersökning, Stockholm, are not sufficiently well preserved to permit a perfectly reliable decision as to whether they may be referred to Bulman's *M. scanicus* Tullberg or rather to *M. parascanicus* Kühne. Therefore it is suggested to retain for these forms the names given by Bulman (1953) and Kühne (1955).

Palaeozoological Laboratory
of the Polish Academy of Sciences
and of Warsaw University
Warsaw, March 1960

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ADAM URBANEK

PRÓBA INTERPRETACJI BIOLOGICZNEJ ZMIAN EWOLUCYJNYCH
W KOLONIACH GRAPTOLITÓW*Streszczenie*

Analiza budowy kolonii w wielu grupach Graptoloidea pozwala stwierdzić, że teki wykazują wzdłuż rabdozomu regularną sukcesję morfologiczną. Różnice morfologiczne tek mogą polegać zarówno na braku lub obecności określonych segmentów teki, jak i na modyfikacjach budowy tego samego segmentu. Te ostatnie wyrażają się stopniem manifestowania się szeregu cech, określających wielkość, kształt i symetrię przydatków aperturalnych. Analiza zmian ewolucyjnych w poszczególnych liniach filogenetycznych wykazuje, że polegają one na stopniowym rozprzestrzenianiu się nowego typu teki, który początkowo występuje tylko w części proksymalnej lub dystalnej. Sposób początkowego manifestowania się nowej cechy nie jest jednak zależny od tego, czy jest ona z morfologicznego punktu widzenia cechą „progresywną” lub „regresywną”. Hipotezy Elles (1922) i Westolla (1950), wysunięte dla objaśnienia zjawisk ewolucji kolonii graptolitów, nie mogą być więc uznane obecnie za wystarczające. Opierając się na nowych badaniach nad graptolitami oraz na danych fizjologii, mechaniki rozwoju i genetyki, autor wysuwa nową hipotezę roboczą, objaśniającą organizację morfofizjologiczną kolonii graptolitów i przypuszczalne mechanizmy zmian genetycznych, jakim podlegały one w procesie ewolucji.

Z biologicznego punktu widzenia, kolonie graptolitów mogą być uważane za całości zwarcie zintegrowane. Integracja osobników zachodziłaby przez dominowanie fizjologiczne ośrodka sikularnego. Dominowanie to realizowałoby się przez rozprowadzanie wytworzonych przez sikulozoida substancji morfogenetycznie aktywnych, zbliżonych do hormonów. Substancje te byłyby rozprowadzane wzdłuż osi kolonii, przypuszczalnie przy pomocy stolonu. Stężenie tych substancji wykazywałoby regularny spadek, czyli gradient wzdłuż osi kolonii. Określona sukcesja astogenetyczna tek, tak charakterystyczna dla wyższych Graptoloidea, znajdowałaby wyjaśnienie w świetle teorii gradientów fizjologicznych, wypowiedzianej przez Childa (1915, 1941) i podjętej przez szereg badaczy. Postać zooida, a co za tym idzie — także teki, byłaby zależna od ilości substancji morfogenetycznych, działających w danej części rabdozomu. Tłumaczy to zarazem regularną sukcesję astogenetyczną tek, w szczególności wśród graptolitów o koloniach dwukształtnych („biform”).

Proces kladogenezy u *Cyrtograptus* Carruthers, zbadany przez Thorsteinssona (1955), pozwala zanalizować sukcesję astogenetyczną tek przy powstawaniu odgałęzień bocznych rabdozomu. Stwierdzono, że pierwsze teki gałęzi bocznej odpowiadają swym typem morfologicznym tekcom bardziej dystalnym, niż wynikałoby to

z ich odległości od sikuli. Zjawisko to można zrozumieć przez analogię ze zjawiskami hamowania wzrostu gałęzi bocznych przez pęd główny u roślin. Podobne przyczyny powodowały opóźnienie w tworzeniu się gałęzi bocznej w stosunku do głównej u *Cyrtograptus*. Ponadto rozwijałaby się ona dopiero po osiągnięciu równowagi w stężeniu substancji aktywnych na wierzchołkach obu gałązek. Tłumaczy to z kolei jednakową postać tek, pączkujących jednocześnie na obu gałązkach. Boczne gałązki stanowiłyby odpowiednio ośrodki dominujące I, II i ewentualnie wyższych rzędów; hamowałyby one tworzenie się pączków na pewnej odległości od siebie, warunkując mniej lub bardziej stałe wzajemne odległości gałązek bocznych dla poszczególnych gatunków *Cyrtograptus*.

Z genetycznego punktu widzenia, kolonia graptolitów może być uważana za pewnego rodzaju klon, tj. zespół organizmów mających ten sam genotyp. Różnicowanie astogenetyczne osobników kolonii stanowiłoby zatem jedynie wyraz różnego fenotypowego przejawiania się tego samego genomu. Ewolucja graptolitów polegałaby na modyfikacjach astogenezy, przy czym (z genetycznego punktu widzenia) odpowiadałyby one zmianom stopnia penetracji i siły przejawiania się (ekspresywności) poszczególnych cech w obrębie kolonii. Zmiany te wywołane byłyby mutacjami genów, kontrolujących powstawanie określonych cech teki, lub zmieniających ilość produkowanych przez sikulozoida substancji morfogenetycznych. Te ostatnie pod względem genetycznym wpływają stymulująco lub hamująco na przejawianie się fenotypowe określonych genów.

Materiał kopalny, w szczególności obraz zmian astogenezy w liniach filogenetycznych dokładniej poznanych, potwierdza w zupełności te założenia teoretyczne. W konkretnych liniach rozwojowych, kolejno po sobie następujące formy różnią się stopniem penetracji i ekspresywności określonych cech. Gdy nowe cechy pojawiają się u przodków początkowo tylko w części dystalnej, obejmując dopiero następnie część proksymalną, należy przyjąć, że modyfikatory warunkują wytwarzanie przez sikulozoida substancji morfogenetycznej, zachowującej się w stosunku do tych cech hamująco. W filogenezie, w wyniku kolejnych mutacji, wzrastałaby aktywność genów lub malałaby aktywność inhibitora. Gdy, przeciwnie, nowa cecha pojawia się u przodków początkowo tylko u tek w części proksymalnej, aby następnie dopiero objąć także teki dystalnej części rabdozomu, należy przyjąć, że modyfikator i zarazem substancja produkowana przez sikulozoida zachowuje się jak stymulator danych cech. W ewolucji takich form wzrastałaby aktywność genów odpowiedzialnych za powstanie odpowiednich cech, lub wzrastałaby aktywność stymulatora.

Analiza zmian ewolucyjnych w konkretnych liniach filogenetycznych wykazuje, że przejawiają się one w określonym zespole cech i utrzymują określony kierunek zmian. Zachowują się one przeto podobnie jak 1) czynniki kumulatywne (modyfikatory), lub też jako 2) allelomorfy wielokrotne, tj. mutacje jednego genu (locus), tworzące serie z różnym efektem fenotypowego przejawiania się i różną aktywnością alleli.

Ogólny mechanizm genetyczny zmian kolonii graptolitów sprowadzałby się zatem do występowania mutacji początkowo słabo przejawiających się fenotypowo, a następnie dopiero zwiększających swą penetrację i ekspresywność. Obraz ten skłania do przyjęcia wniosku, że w wielu szczepach graptolitów ewolucja dokonywała się przez mikromutacje o stopniowo zwiększającym się w szeregu potomków efekcie fenotypowym.

Regularną zmianę postaci kolejnych osobników kolonii, która zdawała się stanowić cechę swoistą graptolitów, można w świetle naszych rozważań zrozumieć jako przejaw bardziej ogólnych prawidłowości biologicznych. Stanowi ona przypuszczalnie wyraz odpowiednich gradientów morfofizjologicznych.

Tak jak przyczyny zmian filogenetycznych organizmów osobniczych zdają się polegać na modyfikacjach ich ontogenezy, tak ewolucja graptolitów jako organizmów kolonijnych zachodziła na drodze modyfikacji astogenezy, tj. przez zmiany sposobu rozwoju kolonii, wyrażające się zmianami poszczególnych osobników. W ostatecznym ujęciu, przyczyny tych modyfikacji dają się sprowadzić do zmian penetracji i ekspresywności czynników genetycznych, przejawiających się w koloniach, stanowiących jednostki podlegające wspólnej kontroli genetycznej.

Z naszych rozważań wynika, że w wielu liniach ewolucyjnych graptolitów, z form pierwotnie uniformicznych powstają formy cechujące się różnym stopniem biformizmu, a z nich — formy wtórnie uniformiczne. W związku z tym, specjalnego rozważenia wymagają rodzaje, grupujące gatunki cechujące się silnym biformizmem — *Demirastrites* Eisel i *Pernerograptus* Přibyl. Proponuje się raczej utrzymać te rodzaje jako reprezentujące określone stadium morfologiczne, poprzez które przechodziła ewolucja wielu linii filogenetycznych, lecz nie wydzielać tych rodzajów w odrębne podrodziny (jak to proponował Přibyl, 1946). Biformiczne rodzaje mniej się różnią od swych wtórnie uniformicznych potomków (*Pernerograptus* Přibyl od *Monograptus* Geinitz, *Demirastrites* Eisel od *Rastrites* Barrande), niż od swych pierwotnie uniformicznych przodków. W pierwszym przypadku różnice są raczej ilościowej natury (stopień penetracji i ekspresywności danych cech), w drugim zaś — bardziej jakościowej (obecność lub zupełny brak danych cech). Odpowiednio do tego proponuje się zaliczenie *Pernerograptus* Přibyl do podrodziny Monograptinae, zaś *Demirastrites* Eisel — do podrodziny Rastritinae.

Do tekstu dodano opis nowych gatunków graptolitów: *Lobograptus simplex* n.sp., *L. exspectatus* n.sp., *Cucullograptus hemiaversus* n.sp. oraz *Cucullograptus aversus rostratus* n. subsp.

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 135)

Przykłady sukcesji astogenetycznej tek u różnych Monograptidae: A *Monograptus argenteus* (Nicholson), B *M. fimbriatus* (Nicholson), C *M. raitzhainiensis* (Eisel), D *M. triangulatus* (Harkness), E *M. communis* (Lapworth). Zarysy rabdozomu $\times 2$, pojedyncze teki $\times 10$; budowa fuzellarna uproszczona (według Bulmana, 1951, 1958).

Fig. 2 (p. 136)

Przykłady sukcesji astogenetycznej tek u różnych Monograptidae, oparte na okazach izolowanych ze skal: A *Cucullograptus hemiaversus* n.sp., B *Saetograptus chimaera* (Barr.), C *Colonograptus colonus* (Barr.), D *Monograptus priodon* (Bronn), E *M.uncinatus* Tullb., F *Pristiograptus dubius* (Suess). W przypadku gdy nie są znane dłuższe fragmenty, przedstawiono kolejno proksymalne, medialne i dystalne teki. Różne głązy narzutowe. A ca $\times 20$, B-F ca $\times 10$.

Fig. 3 (p. 138)

Linia ewolucyjna Monograptidae reprezentująca „progressive series” w ujęciu Elles. Widoczny rozwój i stopniowe rozprzestrzenianie się tek typu „hooked” (1-8); a części proksymalne, b części dystalne (według Elles, 1922).

Fig. 4 (p. 139)

Przykład ewolucji Monograptidae, od form o tekach „hooked” (A) do form o tekach typu pristiograptusowego (C), reprezentujących „retrogressive series” w ujęciu Elles (według Elles, 1922).

Fig. 5 (p. 141)

Schemat ilustrujący rozprzestrzenianie się i zanik tek typu „hooked” w serii „progressywnej” i „retrogressywnej”, według koncepcji „potencjalnej hypermorfozy” Westolla. Postać apertury „hooked” związana jest z odpowiednim stadium wzrostowym teki, jakie osiągać mogą u pewnych gatunków tylko niektóre z nich, u innych zaś wszystkie (według Westolla, 1950).

Fig. 6 (p. 143)

Budowa fuzellarna tek u *Cucullograptus hemiaversus* n.sp. A₁-A₂ teka proksymalna widziana od strony prawej i lewej, B₁-B₂ teka dystalna widziana od strony prawej i lewej (głaz S. 200, Rewal); ca $\times 75$.

Fig. 7 (p. 146)

Porównanie homologicznych odcinków teki Graptoloidea. Metateka graptolitów pozbawionych przydatków aperturalnych (A) reprezentuje tylko segment subaperturalny; metateka graptolitów opatrzonych takimi przydatkami (B) składa się z segmentu subaperturalnego i aperturalnego.

Fig. 8 (p. 153)

Porównanie terminalnych, rosnących części kolonii: A u *Rhabdopleura* (według Lankester, w Grassé, 1948, i Bulmana, 1955; kombinowane), B u *Lobograptus scanicus parascanicus* (Kühne), częściowo rekonstruowane z dwu wzajemnie uzupełniających się fragmentów (głaz S. 137 i 181); st stolon, tz zooid terminalny, n-n+7 kolejne zooidy.

Fig. 9 (p. 153)

Wpływ zmian allometrycznych kształtu tek na postać rabdozomu u Petalograptinae: A *Petalograptus folium* (His.), strona „reverse”; B *Cephalograptus cometa* (Geinitz), strona „reverse”. Oba okazy sprowadzone do tych samych wymiarów długościowych th 1¹ (oparte na fig. 63, 6b, 7b u Bulmana, 1955).

Fig. 10 (p. 159)

Schemat budowy złożonej kolonii *Cyrtograptus*. Teki pączkujące w przybliżeniu jednocześnie połączone liniami przerywanymi (A); B-D schematyczne przedstawienie postaci tek w proksymalnej, medialnej i dystalnej części gałęzi głównej; S sikula, I^o gałązki boczne (cladia) I rzędu, II^o gałązki boczne II rzędu; strzałka pokazuje

miejsce, w którym zachodzi skrócenie gałązki głównej (według Bulmana, 1958; objaśnienia uzupełniono).

Fig. 11 (p. 171)

Schemat ilustrujący: *A-C* rozprzestrzenianie się nowego typu tek od części proksymalnej rabdozomu i interpretację teoretyczną tego zjawiska, *D-F* rozprzestrzenianie się nowego typu tek od części dystalnej rabdozomu i interpretację teoretyczną tego zjawiska; oś *X-ów* — długość rabdozomu, oś *Y-ów* — aktywność substancji morfogenetycznej. Objaśnienia szczegółowe — w tekście.

Fig. 12 (p. 174)

Schemat ewolucji jednej z grup „triangulate monograptids” z dolnej części poziomu *P.gregarius* (d. llandovery, Rheidol Gorge), opracowanych przez Sudbury. Należy zwrócić uwagę na modyfikację tek w linii prowadzącej od *M.triangulatus separatus* do *Rastrites longispinus*. *A-S* kolejne warstwy profilu (według Sudbury, nazwy gatunkowe zaktualizowano).

Fig. 13 (p. 178)

Schemat ilustrujący przypuszczalne stosunki rodowe i typy sukcesji astogenezycznej u *Cucullograptinae*. Uwzględniono kolejno sikulę i pierwszą tekę, teki proksymalne i dystalne każdego gatunku. Oparte na materiałach autora, jeśli nie wskazano inaczej. *A* *Lobograptus simplex* n.sp., *B* *L.exspectatus* n.sp., *C* *L.scanicus parascanicus* (Kühne), *D* *L.scanicus scanicus* (Tullberg), sikula według Walker, 1953; *E* *Cucullograptus hemiaversus* n.sp., *F* *C.aversus aversus* (Eisenack), według Eisenacka, 1942; *G* *C.aversus rostratus* n.subsp., *H* *C.pazdroi* Urbanek. Nad *F* i *G* podano pojedyncze powiększone teki dla wykazania różnic w budowie aparatu aperturalnego.

Fig. 14 (p. 179)

Porównanie części aperturalnych tek, pochodzących w przybliżeniu z tych samych części rabdozomu: *A* *Lobograptus simplex* n.sp., *B* *L.exspectatus* n.sp., *C* *Cucullograptus hemiaversus* n.sp., *D* *C.aversus rostratus* n.subsp.; *1* od strony prawej, *2* od strony lewej. Widoczny wzrost stopnia nasunięcia i podwinięcia płata lewego oraz rudymentacja płata prawego (*A*, *C*, *D*); ca $\times 50$.

Fig. 15 (p. 185)

Interpretacja zjawiska przykracania się septum medialnego w linii ewolucyjnej *Glyptograptus* aff. *persculptus* (Salter), (według Davies, 1929). Na osi *Y-ów* — przypuszczalna aktywność czynnika genetycznego, kontrolującego ilość tek alternujących u 6-ciu kolejnych mutacji tego gatunku (*1-6*); na osi *X-ów* — kolejne teki wraz z zaznaczonym początkiem septum medialnego, właściwym dla poszczególnych mutacji. Septum zaczyna się w tym miejscu rabdozomu, w którym ilość substancji morfogenetycznej spada poniżej poziomu progowego (linia równoległa do osi *X-ów*). Inne objaśnienia — w tekście.

Fig. 16 (p. 186)

Interpretacja zjawiska przykracania się septum medialnego w linii ewolucyjnej *Climacograptus scalaris* var. *normalis* Lapw. (według Waerna, 1948). Na osi *Y-ów* — przypuszczalna aktywność czynnika genetycznego, warunkującego ilość tek alternujących u *Cl. scalaris normalis* (*1-2*), kolejnych mutacji *Cl. scalaris transgrediens* (α - δ), *Cl. medius* (*3-4*); na osi *X-ów* — kolejne teki z zaznaczonym początkiem septum medialnego, właściwym dla poszczególnych mutacji. W prawym górnym

rogu odpowiednie mutacje i ich występowanie stratygraficzne w rdzeniu. Inne objaśnienia — jak fig. 15, i w tekście.

Fig. 17 (p. 188)

Seria wyrostków aperturalnych w grupie *Saetograptinae*, reprezentująca kolejne stadia redukcji perydermy wyrostka: *a-b Colonograptus cf. colonus* (Barr.), *c* postać morfologicznie przejściowa między *Colonograptus* i *Saetograptus* (transient), *d-e Saetograptus chimaera chimaera* (Barr.), (w pojęciu Urbanka, 1958), *f S.chimaera cervicornis* Urbanek, *g-h S.chimaera cf. cervicornis* Urbanek, *i-j S.chimaera cf. salweyi* (Hopk.). Granica między wyrostkiem i jego podstawą zaznaczona linią zgrubiałą; granice fuzellusów źle widoczne lub konwencjonalnie zaznaczono liniami przerywanymi. Wszystkie wyrostki reprezentują th 1 młodych rabdozomów (głazy S. 19, S. 36, S. 38, S. 54, S. 149, S. 201); ca $\times 50$.

Fig. 18 (p. 192)

Postacie modalne skrzydełek i przezmianek (halteres) we wszystkich możliwych kombinacjach allelomorfów serii „vestigial” u *Drosophila*, jako przykład morfologicznego obrazu alleli wielokrotnych; *nw* no wing, *vg* vestigial, *no* notched, *ni* nicked, *+vg* wild type. Poniżej procenty penetracji i wartości określające względną potencję (aktywność) danej kombinacji genów (według Mohra, 1932).

Fig. 19 (p. 212)

Budowa tek u *Lobograptus simplex* n.sp. *A* budowa fuzellarna teki dystalnej; *1* z prawej strony, *2* z lewej strony; *B* część aperturalna teki dystalnej, od strony wentralnej; *C* część aperturalna teki dystalnej, od strony dorsalnej; *D* część aperturalna teki dystalnej, od góry (głaz S. 219, Lubin), ca $\times 70$.

Fig. 20 (p. 213)

Budowa fuzellarna płata aperturalnego u *Lobograptus simplex* n.sp., na przykładzie odpreparowanego i odbarwionego płata prawego; *A* z boku, *B* od góry (głaz S. 219, Lubin); ca $\times 105$.

Fig. 21 (p. 217)

Zmienność astogenetyczna tek u *Cucullograptus aversus rostratus* n.subsp. *A* pierwsza teka, *B* teka medialna, *C* teka bardziej dystalna, wszystkie widziane od strony lewej; *m* dodatkowa błona na ścianie wentralnej (wiercenie Mielnik n. Bugiem, głęb. 925 m), ca $\times 70$.

Pl. I

Lobograptus simplex n.sp., fragment medialnej części rabdozomu: *1a* od strony prawej, *1b* od strony lewej, *1c* wentralnie (głaz S. 219); ca $\times 15$.

Pl. II

Fig. 1. *Lobograptus exspectatus* n.sp., fragment medialnej części rabdozomu: *a* od strony prawej, *b* od strony lewej (głaz S. 218); ca $\times 15$.

Fig. 2. *Cucullograptus hemiaversus* n.sp., fragment części dystalnej rabdozomu: *a* od strony prawej, *b* od strony lewej (głaz S. 200); ca $\times 15$.

Fig. 3. *Lobograptus exspectatus* n.sp., budowa fezellarna płata aperturalnego, oparta na wypreparowanym i odbarwionym płacie prawym, widzianym *a* z boku, *b* z góry (głaz S. 218); ca \times 95.

Fig. 4. *Lobograptus exspectatus* n.sp., rekonstrukcja wyglądu płata aperturalnego w postaci rozpostartej w jednej płaszczyźnie. Oparte na fig. 3 *a-b*; ca \times 95.

Pl. III

Fig. 1-5. *Cucullograptus aversus rostratus* n.subsp., teki i aparaty aperturalne od bardziej proksymalnych do bardziej dystalnych, widziane *a* od strony prawej, *b* od strony lewej (1-2 głaz S. 121, 3-5 głaz S. 205); ca \times 40.

Fig. 6. *Cucullograptus aversus aversus* (Eisenack), reprodukcja fragmentu według Eisenacka (1942, pl. 2, fig. 1), teka dystalna; ca \times 40.

АДАМ УРВАНЭК

ПОПЫТКА БИОЛОГИЧЕСКОЙ ИНТЕРПРЕТАЦИИ ЭВОЛЮЦИОННЫХ ИЗМЕНЕНИЙ В КОЛОНИЯХ ГРАПТОЛИТОВ

Резюме

Основываясь на новейших исследованиях граптолитов и данных физиологии, механики развития и генетики, автор представил новую рабочую гипотезу, объясняющую морфологическую организацию колонии граптолитов и возможные механизмы генетических изменений, каким подвергались эти колонии в процессе эволюции.

У многих Graptoloidea теки проявляют вдоль рабдосомы правильную морфологическую последовательность. Проявляется она в постепенных видоизменениях строения тек, которые могут состоять в отсутствии или присутствии соответствующего сегмента теки, равно как на различных видоизменениях строения этого же сегмента тек. Характер этих астогенетических видоизменений допускает предположение, что они — согласно с известной теорией Чайльда (Child, 1915, 1941) — являются проявлением соответственных морфофизиологических градиентов. Соответственно этому, колония граптолитов проявляет некоторую полярность своей организации. Определялась она повидимому способом выработки и распространения известных морфогенетических субстанций, определяющих строение последовательных зооидов. Эти субстанции, вырабатываемые вероятно сикүлозоидом, распространялись бы вдоль рабдосомы, проявляя определенный градиент. Сикүлозоид составлял тут вероятно

центр, физиологически доминирующий над остальными особями колонии. Эта гипотеза применима равно как для одноосевых, так и многоосевых (*Cyrtograptus*) колоний граптолитов. Главная ветвь и последовательные боковые ветви у *Cyrtograptus* следует считать как разного порядка доминирующие центры, контролирующие последовательный темп почкования и обуславливающие морфологическую последовательность в теках боковых ответвлений.

Как установлено в ряду филогенетических линий Graptoloidea, эволюция состоит в последовательном распространении вдоль рабдосомы нового типа тек, который первоначально проявляется только в проксимальной либо дистальной части. Так как колония граптолитов составляет некоторого рода клон, поэтому астогенетические различия между особями колонии являлись единственно проявлением разного фенотипического выражения того же самого генома. Эволюция граптолитов основывалась бы на астогенетических модификациях, которые в отношении генетическом составляли бы изменения степени пенетрантности или процента проявления, и степени выражения или экспрессивности генетических факторов в пределах колонии. Изменения эти вызваны были повидимому мутацией генов, контролирующей возникновение определенных признаков теки или изменяющих количество вырабатываемых сикүлозоидом морфогенетических субстанций. Эти последние в генетическом отношении влияют стимулирующе либо сдерживающе на фенотипическое проявление определенных генетических факторов, т. е. ведут себя как зависящие от определенных генов-модификаторов. Когда у предков новые признаки появляются первоначально лишь в дистальной части, только потом обнимая и проксимальную часть, следует принять, что модификаторы обуславливают вырабатывание сикүлозоидом морфогенетической субстанции, ведущей себя в отношении фенотипического проявления этих признаков как ингибитор. В филогенезисе, в результате последовательных мутаций, возрастала бы активность генов, ответственных за возникновение определенного признака, либо уменьшалась бы активность ингибитора. Когда же новый признак появляется у предков в начале только в проксимальной части, следует принять, что модификаторы, а вместе с тем и субстанция, вырабатываемая сикүлозоидом, ведет себя как стимулятор фенотипического проявления данных признаков. В эволюции таких форм возрастала бы активность генов, определяющих данный признак, или возрастала бы активность стимулятора. Анализ эволюционных изменений в конкретных филогенетических линиях указывает, что они проявляются в определенной совокупности признаков и сохраняют определенное направление. Ведут они себя поэтому как 1) кумулятивные факторы (модификаторы), или же как 2) множественные аллеломорфы, образующие серии аллеломорфов с различным эффектом фенотипического проявления и различной морфогенетической активностью.

Общий генетический механизм изменений колонии граптолитов состоял бы, следовательно, в проявлении мутаций, первоначально слабо проявляющихся

фенотипически, и только последовательно увеличивающих свою пенетрантность и экспрессивность.

В работе обсуждаются также таксономические последствия нового воззрения на организацию колонии граптолитов, на вероятные генетические механизмы их эволюционных изменений и добавлены описания новых видов граптолитов: *Lobograptus simplex* n. sp., *L. exspectatus* n. sp., *Cucullograptus hemiaversus* n. sp. и *C. aversus rostratus* n. subsp., упоминаемых в тексте.

EXPLANATIONS OF PLATES

Pl. I

Lobograptus simplex n.sp.

Fragment of the medial part of rhabdosome: 1a right side view, 1b left side view, 1c ventral view (boulder S. 219); approx. $\times 15$.

Pl. II

- Fig. 1. *Lobograptus expectatus* n.sp., fragment of medial part of rhabdosome: a right side view, b left side view (boulder S. 218); approx. $\times 15$.
- Fig. 2. *Cucullograptus hemiaversus* n.sp., fragment of distal part of rhabdosome: a right side view, b left side view (boulder S. 200), approx. $\times 15$.
- Fig. 3. *Lobograptus exspectatus* n.sp., fusellar structure of apertural lobe, based on isolated and transparent right lobe: a lateral view, b top view (boulder S. 218); approx. $\times 95$.
- Fig. 4. *Lobograptus exspectatus* n.sp., reconstruction of apertural lobe spreading on a plain; based on fig. 3 a, b; approx. $\times 95$.

Pl. III

- Fig. 1-5. *Cucullograptus aversus rostratus* n.subsp., thecae and apertural apparatus in more proximal and more distal thecae: a right side view, b left side view (1-2 boulder S. 121, 3-5 boulder S. 205); approx. $\times 40$.
- Fig. 6. *Cucullograptus aversus aversus* (Eisenack), (reproduction of a fragment from Eisenack, 1942, pl. 2, fig. 1), distal thecae; approx. $\times 40$.



1 a



1 c



1 b



1a



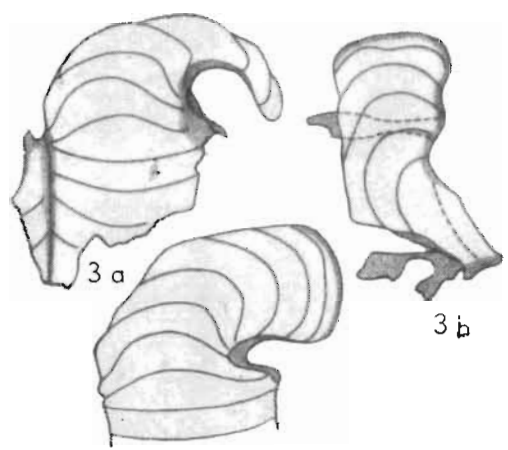
2a



2b



1b



3a

3b

4

