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MAJOR ASPECTS OF EVOLUTION OF THE GRAPTOLITES

Abstract. — The sequences of graptolite faunas, originations and extinctions, origin of new morphological types, and palaeobiogeographical provinces are aspects of graptolite evolution which may be interpreted in terms of their essential coloniality, their change from benthos to plankton, inbreeding and outbreeding, genetic polymorphism and in terms of anagenetic and cladogenetic grades.

Within this framework several topics are discussed which have been variously favoured over the years by neontologists and palaeontologists alike, to wit: neotony, paedomorphosis and recapitulation; adaptiveness and preadaptation; phyletic gradualism and punctuated equilibria; mosaic evolution, convergence and parallelism; orthogenesis, programme evolution and the theory of trends; penetrance and expressivity of biocharacters; and Cope's Rule.

Some of these are rejected as untenable in a modern context and the others are considered against the evolutionary patterns peculiar to graptolites, and their major adaptive trends through time.

INTRODUCTION

It is not facile to remark that due regard for stratigraphical evidence is fundamental to a palaeontologist's deductions concerning graptolite evolution. For example, *Glyptograptus* precedes both *Dicellograptus* and *Dicranograptus* in time so that the once tempting morphological sequence of *Dicellograptus* — *Dicranograptus* — *Glyptograptus* is impossible as an evolutionary sequence. Such statements cannot be made with confidence until the amount of stratigraphic information is sufficient to indicate that it is highly unlikely that occurrences of *Dicellograptus* and *Dicranograptus* will be found stratigraphically earlier than those of *Glyptograptus*. In the recent past both Professors Bulman and Kozłowski leaned heavily upon an understanding of the morphology of the graptolites, rather than on a precise stratigraphy. Such a precise stratigraphy was not available to them, except in certain sections, whilst the problems concerning morphology were perhaps even more pressing at the time. Even today much more useful data on Ordovician stratigraphy is needed;

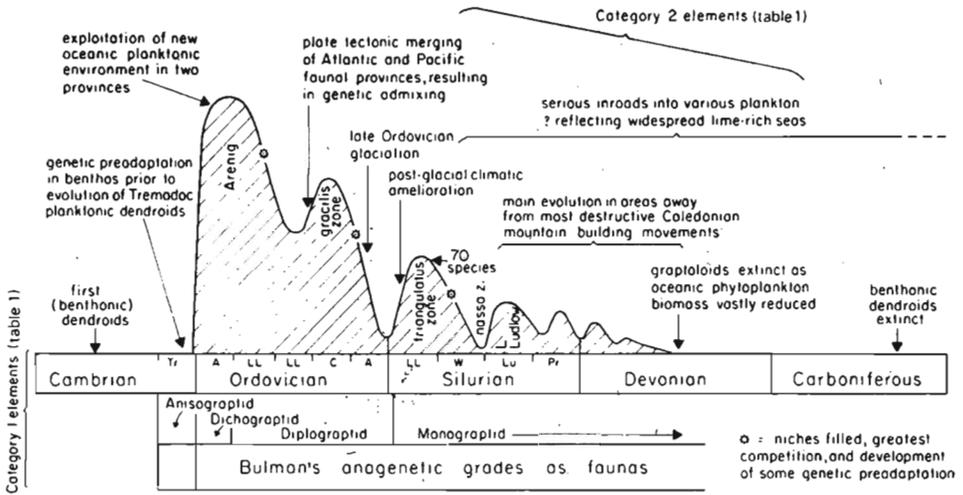
but whilst detailed morphological work will always be essential the labours of Kozłowski and Bulman in particular have spectacularly reduced the size of that particular mountain. Their work, for example, that of Bulman on developmental stages of graptoloids (*bifidus*, *extensus*, *leptograptid* stages etc.) could not be, and is not, wholly correct simply because each newly isolated graptolite seems to introduce new complexities, quite apart from the fact that the stratigraphic horizon was often in doubt. The work of Kozłowski and Bulman can be strongly contrasted in these respects with more recent work by, for example, Urbanek (1966, 1976) or the present author (1970, 1972, 1976) where morphological changes are readily related to a stratigraphical sequence. One of the more recent discoveries is that the *Glyptograptus* — *Dimorphograptus* — *Atavograptus* morphological series is a highly unlikely evolutionary series since *Atavograptus* precedes *Dimorphograptus* by as much as two graptolite zones and must have originated relatively suddenly from the fully biserial genus. The relatively sudden appearance of new types is further alluded to below, as is the later apparently abortive attempt (by *Dimorphograptus*) to achieve the uniserial state, both events are quite like the appearance of *Dicranograptus* at a much later date than the Arenig *Glyptograptus*. Both features help to build a picture of graptolite evolution which may not readily fit the evolutionary interpretive theories of neontologists.

ORDERING THE MODEL

Some of the terminology used by neontologists, not to mention the interpretive theory, has been both difficult to understand and difficult to recognize from a palaeontological standpoint. The converse is also true, and some attempt is made here to classify and identify the various concepts which fall broadly into three categories.

First of all are those ideas which could be said to be directly related to the rock record or which might reasonably be said to be recorded in the rock. Here I would include the relative range in time of genera and species; the overall sequence of faunas (perhaps including here such sinful concepts as various types of graptolite zones; anisograptid, dichograptid etc. faunas); recording of originations and extinctions; origin of new morphological types; and the recognition of palaeobiogeographical provinces. All of these depend heavily upon data recorded from accurately measured and collected sections, and upon the principles of stratigraphy in correlating these sections prior to synthesis of the data.

The second category of concepts are those of probable factual nature which must be borne in mind whilst deducing any evolutionary model. Included here would be recognition of the essential coloniality of graptolites; the concepts of rhabdosomal astogeny and thecal ontogeny;



the change from graptolites as benthos to graptolites as macrozooplankton; the possibility of ice ages reducing the tropical plankton biomass; plate tectonics; genetic polymorphism; inbreeding and outbreeding. These,

Table 1
 GEOLOGIST/PALAEONTOLOGIST → ← NEONTOLOGIST

Terms used with direct reference to rock record	Factors bearing on evolutionary interpretations	interpretative theory
relative ranges of species and genera sequence of faunas originations and extinctions origin of new types palaeobiogeographical provinces etc.	essential coloniality astogeny/ontogeny benthos to plankton changes inbreeding/outbreeding genetic polymorphism ice ages/ latitudinal thermal gradients plate tectonics/oceanic configurations etc.	recapitulation programme evolution orthogenesis penetrance & expressivity of morphogenetic substances neotony/paedomorphosis Cope's rule preadaptation & adaptiveness & adaptive peaks theory of trends mosaic evolution punctuated equilibria & phyletic gradualism dithyrial populations habitats & microhabitats anagenesis/cladogenesis etc.
Category 1	Category 2	Category 3

as well as the recording mechanics of burial are the forces shaping the patterns and processes we are attempting to deduce in category 3 above.

Category three largely includes recognition of the patterns of evolution and the interpretive theory by which we explain them. Here we would discuss neotony and paedomorphosis; recapitulation; orthogenesis; mosaic evolution, convergence and parallelism; phyletic gradualism and punctuated equilibria; adaptiveness and preadaptation; programme evolution and the theory of trends; penetrance and expressivity; Cope's Rule and cladogenesis and anagenesis.

Arranged on a diagram (Table 1) with category 1 to the left and category 3 to the right we can envisage the geologist/palaeontologist beginning from the left of the diagram and the neontologist beginning from the right, each using rather different tools, the one patterns in the rock, the other neontological theory based upon present day studies of evolutionary mechanisms. We can imagine the two approaches coming together at some point and possibly producing some conclusion concerning categories 2 and 3 if not category 1.

UNTENABLE OR OBSOLETE CONCEPTS

Some of the concepts listed above have been discussed elsewhere by Rickards (1977) and are not considered in detail here. It was considered that there was no evidence from graptolite astogeny or thecal ontogeny to support the recapitulation hypothesis (that ontogeny or astogeny reflects phylogeny) programme-evolution (Lang 1923; Bulman 1933) and orthogenesis, both of which implied a "predetermined" and inexorable course for a set of coeval trends in demonstrably different lineages, were regarded as obsolete concepts the facts pertaining to which could be more readily encompassed in modern ideas about evolutionary trends. Similarly Urbanek's (1960) concept of penetrance and expressivity of a morphogenetic substance along the rhabdosome from the siculo-zoid, resulting in gradients of morphological expression is perhaps inadequate, not because morphogenetic substances are unlikely to be produced but because their production to such a regular plan for each species suggests a more important underlying genetic control (Prof. J. W. Valentine, pers. comm.). In this instance it is a question of emphasis rather than correctness or otherwise.

CONCEPTS OF LESSER IMPORTANCE

Several examples of paedomorphosis (and, therefore, possible neoteny) were adduced by Rickards (1977), for example *Orthograptus* sp. — *Petalograptus* spp. — *Cephalograptus* spp; *M. sedgwickii* — *M. halli*; *Iso-*

graptus — *Corynoides*; *Glossograptus* — *Nanograptus*. Probably other similar cases will be disclosed by further research, and certainly some cases of stipe reduction (one of Elles' trends) need further study, but none of these possibly paedomorphic evolutionary lineages appear to give rise to major revolutionary expansions in terms of species and genera.

Cope's rule, that increasing robustness in lineages preceded extinction, is only very loosely applicable to graptolite evolution for although the inception of new morphological types was often through slender species, extinction of major lineages is often preceded by further diminutive forms or, alternatively, these forms give rise suddenly to quite new genera (e.g. *Colonograptus*).

MAJOR CONCEPTS

In modern geneticists's terminology some of the bigger steps in graptolite evolution were so spectacularly successful (in terms of replacement success) that the preadaptation must have been nearly perfect. Examples might be the change from benthonic dendroids to planktonic dendroids or of uniserial scandent graptoloids from biserial scandent forms. By contrast some seemingly small features (the graptolite virgella) were originally selected, and persisted in such a striking manner that they must have remained on an adaptive peak and been continuously selected (adaptiveness). The function of such structures is in need of close examination for they are surely of import.

The successful occupation of a new niche was followed by rapid speciation, as with the first graptoloid plankton for example. The evolving lineages were then subjected to what may have been lesser environmental pressures, at least for long periods of time. Alternation of habitat or microhabitat could subject representatives of different lineages to similar pressures, so that morphological changes could take place at more or less the same time in more or less the same fashion, but in different lineages. Such changes are encompassed by the theory of trends concept, and as such the term trend is useful. A considerable number of such trends were identified by Rickards (1977), but the habitat requiring proximal end protraction for example, almost simultaneously in the genera *Akidograptus*, *Orthograptus*, *Rhaphidograptus*, and others, is at present a matter for speculation (? different depths, light zones, etc.) and in the future a matter for investigation.

Over-printed upon this pattern of trends, and at times difficult to unravel from it, is a tendency for different biocharacters to evolve and change at different rates in the same and in other lineages. This has been termed mosaic evolution. It is beyond question a valuable concept for

graptolite evolutionary studies and many examples can be found, particular at the time that the new niche is being first exploited. An excellent example is in the early Silurian where seven different biocharacters (small sicula; glyptograptid thecae; thecal elongation; thecal process growth; thecal introversion, extroversion and simplification) help to define the mosaic of six evolving and related genera: *Atavograptus*, *Pribylograptus*, *Coronograptus*, *Lagarograptus*, *Monograptus*, and *Prisio-graptus* to list them in order of appearance. But thecal extroversion, and thecal introversion, both effect several other genera at the same time, establishing that the two concepts of trends and mosaic evolution are useful and probably valid.

At several points in this paper rapid evolutionary steps have been implied. It seemed to Rickards (1977) that what Eldredge and Gould (1972) termed punctuated equilibria for their allopatric model was a more fitting description of graptolite evolution than one of phyletic gradualism. Indeed gradual changes in specific lineages are extremely difficult to find. In a graptoloid-rich plankton peripherally isolated parts of a population may occur, perhaps related to latitudinal thermal gradients, but isolation could also occur in the form of microhabitats, as would be created by depth distribution for example. A not dissimilar example from the present day would be the microhabitats of *Turdus philomelos* and *T. viscivorus*. The identification of microhabitats for graptolite plankton is clearly of importance despite the attendant difficulties. Instances of the rapid appearance of new morphological types are common at all taxonomic levels: benthonic dendroids to planktonic dendroids; the origin of biserial scandent graptoloids; the origin of uniserial scandent graptolites.

Other facets of faunal change imply the presence in the graptolite-rich planktonic environment of habitats as yet unidentified. For example the successive occurrence of not dissimilar rhabdosomes of quite different evolutionary origins. Thus from the Ordovician to the Devonian is a succession of slender, spread, ramose rhabdosomes, usually just a small number of species at each horizon: *Amphigraptus*, *Pleurograptus*, *Diversograptus*, *Cytograptus carruthersi*, *Linograptus* and *Abiesgraptus*. Similar sequences can be deduced for cyrtograptids; for uniserial scandent forms (*Parazygograptus*, *Peiragraptus*, "*Monograptus*"); for multi-serial scandency; for spiral rhabdosomes; for thecal types and so on. It seems likely that this convergence indicates the availability in any one oceanic plankton biomass of numerous habitats or microhabitats which persisted, possibly discontinuously, for much of the Palaeozoic.

The same question can be looked at in another way. If such niches persisted and the species were successfully pre-adapted, why did successive species and genera die out? Perhaps this suggests microhabitats rather than habitats. What changes in habitat caused the extinction of such a successful morphological type as the biserial scandent rhabdosome

(Arenig to Ludlow)? Later biserial stipes ("abnormal specimens") occur in some assemblages of monograptids (Prof. A. Urbanek, pers. comm.) but although these would exist as, in effect, dithyrial populations the uniserial scandent stipe persisted, suggesting that the relevant environmental change took place at the base of the Silurian in the *persculptus* Zone.

Finally in this section the concepts of anagenesis and cladogenesis (Huxley 1958; George 1962; Bulman 1963; Rickards 1977) should be examined more thoroughly. Rickards, (*op. cit.*) expressed some doubts about their recognition when applied to graptolite evolution. What are "major" morphological changes in the early Ordovician (stipe reduction and branching) are not possible in the Silurian where the "major" events are often thecal changes. On the other hand future studies of Ordovician graptolites (dendroids and graptoloids) will almost certainly reveal much greater thecal variation than previously supposed. If this happens the relegation of thecal variation to cladogenetic or "minor" or "divergent" processes could well be justified. Rickards (1975, 1977) attempted to give a broad evolution-cum-mode-of-life interpretation of the succession of graptoloid faunas (Elles 1922; Bulman 1958; Bulman 1963) as did Kirk (1969). Both views implied the general and major "biological improvement" required by Huxley's (*op. cit.*) concept of anagenesis. It would be unduly cynical to conclude that this general biological improvement led to their extinction before the ancestral groups became extinct (the benthonic dendroids) for the graptoloids surely occupied the planktonic niche successfully and for a long time. The most reasonable conclusion is that their particular habitat became extinct before they did! But these latter questions are to be dealt with by others at this conference.

MAJOR EVOLUTIONARY EVENTS

Figure 1 idealizes the abundance of species of the graptoloids from the Arenig until their extinction in the Devonian. Figures for the Ordovician are necessarily approximate but the Llandovery peak (about *triangulatus* Zone) is composed of some 70 species, and the relative proportion of the curves is perhaps correct. Beyond question the curves represent a series of evolutionary explosions of diminishing size, alternating with troughs which include two near-extinctions of the planktonic graptoloids in the late Ordovician and late Wenlock. The following conclusions and remarks may be made, and where possible related to the foregoing principles and concepts:—

1. The genetically preadapted dendroid benthos gave rise in the late Cambrian (Tremadoc) to the planktonic dendroids.

2. Responses to the new oceanic planktonic environment involved a rapid transition to the graptoloids with loss of bithecae, reduction of stipe numbers, reduction of cortical periderm and several other trends (for details see Rickards 1975, 1977), and probably also a general change to an hermaphroditic breeding strategy.

3. Successful exploitation of the new niche is spectacularly confirmed by the great speciation represented by the Arenig peak. This took place in two faunal provinces, the Atlantic and Pacific (see Skevington 1974 for a full summary). After the initial diversification there was a gradual "decline" through the Llanvirn.

4. The second evolutionary explosion at about *gracilis* Zone times was almost certainly a result of the genetic admixing of the provincial faunas which took place in the Caradoc perhaps as a result of gradual closure of the so-called proto-Atlantic ocean, perhaps in part due to the onset of the Ordovician glaciation which reached its acme in the late Ordovician.

5. The late Ordovician evolutionary "low" was probably a result of the glaciation seriously reducing the areal extent of warm tropical seas in which the graptoloids flourished. The graptoloids are represented by very few species and genera in the latest Ordovician and very nearly became extinct at this time.

6. Each of the Ordovician explosive peaks is characterised by many trends and by examples of mosaic evolution. In some cases, as with the rapid appearance of biserial scandent forms in the Arenig, the initial environmental pressures waned (or the niches became filled) and major evolutionary steps were followed by abortive attempts to achieve the same end (*Dicranograptus* as opposed to *Glyptograptus*).

7. The Llandovery diversification was a result of amelioration of the climate following the ice age, coupled with the widespread development of, at first, shallow, warm but deepening seas. The remarks under 6 above also apply here and events have been studied in some detail (e.g. Rickards *et al.* 1976).

8. The decline of the graptoloid plankton in the late Wenlock is a more puzzling evolutionary "low", but it is clear that the graptoloids were even closer to being extinct in the *nassa* Zone than in the late Ordovician. The plankton as a whole may have suffered through the very widespread development of lime-rich, tropical seas which reached a considerable areal extent in the *nassa* to *ludensis* Zones. At the same time there is widespread evidence of basinal instability reflected by slumping of calcareous muds, perhaps heralding the final act in the closure of the proto-Atlantic ocean.

9. In areas where infilling of the geosynclines occurred later (as in the Ural region, for example) the graptoloids survived into the Devonian, but in Britain graptoloids are rare by *leintwardinensis* Zone times and become locally extinct following the *Bohemograptus* proliferation zone.

It is conceivable that the oceanic phytoplankton in this latter region was seriously depleted and hence the probable food supply of the zooplankton removed.

10. In the Devonian and early Carboniferous the geological record indicates a poor plankton, and what happened in Britain in the Ludlow may have become widespread at later periods elsewhere. The graptoloids may have become extinct as the phytoplankton biomass was seriously reduced. Several questions related to this problem are dealt with elsewhere in the conference and will not be elaborated here.

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DISCUSSION

A. Lenz:

1. Arenig peak—result of summation of total diversity of two zoogeographic provinces, whereas late Ordovician and Silurian diversity is only from a single zoogeographic province. Therefore one would expect an apparent greater total diversity of Arenig graptolites.
 2. Comment relating to late Wenlock “crisis”—throughout Arctic and Cordilleran North America, Wenlock times reflect widespread shallowing conditions. This shallowing could increase environmental pressure and lead to many extinctions, if on a greater-than-continent size.
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