THE EMERGENCE AND EVOLUTION OF LINOGRAPTIDS

ADAM URBANEK

Urbanek, A. 1997. The emergence and evolution of linograptids. *In:* A. Urbanek and L. Teller (eds), Silurian Graptolite Faunas in the East European Platform: Stratigraphy and Evolution. — *Palaeontologica Polonica* **56**, 233–269.

Macroevolutionary effects due to anagenetic changes within a single lineage have been traced in the Linograptinae from Late Wenlock single-stiped Lobograptus? sherrardae, through bipolar Neodiversograptus and multibrachiate Linograptus, to Early Devonian compound colonies of Abiesgraptus. The ability to generate a number of sicular cladia improved the stability of the rhabdosome, and, in the evolution of *Linograptus*, the resulting geometrical constraints were overcome by diverting their growth. The main lineage is subdivided into four chronospecies displaying periods of fairly high abundance and a distinct morphological norm. These periods were separated by intervals of comparative scarcity, probably related to the bottlenecking of the lineage. The only instance of change in large populations is the L. posthumus-A. tenuiramosus phyletic transition. Speciation events (transformations) seem to be governed by the mechanisms of transient polymorphism, whilst periods of relative persistence of the norm were probably related to microevolutionary changes in monomorphic populations. A disparate origin of unit characters within the complex Abiesgraptus pattern is suggested. These characters appeared independently and heterochronously within the populations over the entire range of distribution of the ancestral species to be later assembled into a single adaptive syndrome. Cosmopolitan distribution of both the ancestral and the daughter species implies a polycentric or a pantopic emergence of the Abiesgraptus.

Key words: Linograptinae, multiramous colonies, phyletic evolution, macroevolution, adaptive syndrome.

Adam Urbanek, Instytut Paleobiologii PAN, ul. Twarda 51/55, 00-818 Warszawa, Poland.

Received 13 March, accepted 30 June 1995



ADAM URBANEK

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INTRODUCTION

In the last decades much attention has been paid to macroevolution as opposed to speciation, and especially, to microevolutionary events. Theoretical considerations on the mechanisms involved in macroevolutionary changes can certainly be illuminating, but empirical examination of the instances of macroevolution as represented in the fossil record has always been of crucial importance. It provides a starting point for speculations as well as the criteria for the falsification of the hypotheses and explanations proposed.

The origin of the multiramous graptolite colonies within the subfamily Linograptinae is a graphic example of macroevolution, perfectly suitable for a case study. Moreover, the generation of compound colonies may be regarded as the most conspicuous event in the late history of the Graptoloidea.

Morphologically, the net result was transformation of the one-stiped monograptid rhabdosome into a multiramous one, achieved through the budding of a number of secondary branches radiating from the aperture of the sicula. This structural foundation was further developed by the formation of lateral cladia on some of the stipes. The taxonomic effect was the appearance of three genera (*Neodiversograptus*, *Linograptus*, and *Abiesgraptus*) forming a separate subfamily, the Linograptinae. The ecological results involved the formation of a novelty – in the form of compound rhabdosomes probably adapted to living in low energy waters. This was a great evolutionary success, and such colonies were flourishing in the Late Silurian–Early Devonian seas.

In every respect, therefore, the emergence of linograptids represented the transspecific level of evolutionary changes. What is more, the case of the Linograptinae illustrating the mesoscale of changes is especially instructive as it enables tracing the relations between sequential speciation and macroevolutionary processes proper. In addition to the analysis of the record, the aim of the present paper is to provide a conceptual framework for understanding of the processes involved.

DEFINITION OF THE PROBLEM

The change from the standard one-stiped monograptid rhabdosome to the multiramous compound colony may be visualized as an instant process. The appearance in a siculozooid of an ability to produce more than just a single daughter zooid by means of simultaneous budding seems morphogenetically a relatively simple event, a possible result of a single mutation with a considerably large phenotypic effect.

A similar mode of budding is represented by some cephalodiscid pterobranchs, e.g. by *Cephalodiscus gracilis*, where an adult zooid is capable of an almost simultaneous budding of a number of daughter individuals. They form a stellate group of buds in different growth stages (HARMER 1905: pl. 1, fig. 4 therein), thus providing a living model of morphogenesis in the *Linograptus* colonies (URBANEK 1963).

However, the emergence of linograptids followed a different pathway, that of stepwise generation of a multiramous condition. The fossil record available indicates that compound *Linograptus* colonies were preceded by pauciramous forms, chiefly represented by two-stiped bipolar colonies of the ancestral species – *Neodiversograptus nilssoni*. It therefore seems safe to stipulate that the "technology" applied in the macroevolutionary processes within the Linograptinae was piecemeal rather than total, stepwise rather than instant, producing a cumulative effect as a result of some partial improvements (see, however, RICKARDS *et al.* 1994 for a different opinion as well as p. 242 herein).

Another important feature of the linograptid phylogeny is its being restricted to a single line of descent. All morphological changes were realized in one lineage, practically without splitting. Almost all species belonging to the Linograptinae were sequential (chronospecies) and, consequently, no real multiplication of species is to be found (see p. 162 for a detailed discussion).

The idea that phyletic evolution in a single lineage may bring about macroevolutionary effects has fallen in disgrace mainly due to the wide acceptance of the punctuational model of phylogeny. As stated by STANLEY (1979: p. 17), "the punctuational model does not deny the existence of phyletic evolution, but relegates this mode of change to a subordinate role". Moreover, there is a strong conviction that "the speciational component of evolution so outweighs the phyletic component, in general, that it accounts for a large majority of transitions between genera. The role of phyletic evolution in the origin of families and orders is even smaller" (STANLEY 1979: p. 19). Recently this view has been strengthened by JACKSON *et al.* (1990), who claim that no anagenetic advances have ever been recorded in the evolution of a single monophyletic lineage. GOULD (1990) approves this conclusion as "a strong point", and similar ideas seem to prevail presently, with the notable exception of HOFFMAN (1988). He did not exclude that macroevolutionary effects may be attained within a single line of descent, quoting as an example my earlier studies on the Linograptinae (URBANEK 1963, see also LEVINTON 1986).

It is difficult to say whether the presently prevailing assessment of the significance of phyletic and speciational changes for transspecific evolution is generally adequate, but it may well be. Unfortunately, there is something in the very nature of scientific ideas that makes them universally accepted in their most extreme form. Punctuationalism is no exception to this rule. Hopefully, the present case study revealing the great role of phyletic evolution in shaping the major features of a large group of fossil animals may provide stimulative evidence for the ongoing debate about the mechanisms and the course of macroevolution.

MATERIAL AND METHODS

The material analyzed herein contains not only the samples previously etched out from the Mielnik IG-1 borecore and described in URBANEK (1963), but also some additional ones obtained from the Přidoli age section of the core.

More material was obtained from newly collected and dissolved erratic boulders coming from the locality Rewal and numbered S.236 in the author's collection, as well as from S.22 boulder (Jarosławiec, the collection of Dr. A. KOZŁOWSKA-DAWIDZIUK, Institute of Palaeobiology PAN, Warszawa), referred to as sample A further on. Whilst S.236 contained typical *Neodiversograptus nilssoni* and its age may be defined as the *N. nilssoni* Zone, the boulder marked S.22 in A. KOZŁOWSKA-DAWIDZIUK collection contained a transient form, *N. nilssoni/N. beklemishevi*, identified herein as *N. cf. beklemishevi*. Graptolites from this boulder were described by A. KOZŁOWSKA-DAWIDZIUK in her MSc thesis (unpublished). The associated fauna (*Lobograptus parascanicus, Cucullograptus pazdroi, Saetograptus chimaera*) is indicative of what is currently defined as the *L. scanicus* band.

Sample B corresponds to linograptid remains etched from the Mielnik borecore at a depth of 934.50 m (the *S. leintwardinensis* Zone) and representing a transient *N. beklemishevilL. posthumus.*

Thus samples A and B contained transients while the bulk of the material may be assigned to one of the well-defined chronospecies of the Linograptinae.

The methods used may be defined as an inductive approach to the study of phylogeny, which means tracing morphological changes in the sequential series of samples obtained from succeeding horizons. Following a modern wording, it can also be called stratophenetic (GINGERICH 1976). However, the use of morphometric and statistical methods has been strongly restricted by the small numerical size of the samples. This cannot be overlooked as an important limitation of the material presented herein.

Although based on real specimens, all figures are presented diagrammatically in order to illustrate generalized concepts rather than factual data. They are completed by ideograms illustrating the working hypothesis advanced in the present paper.

Scanning electrone micrographs were taken from gold-platinum-coated isolated specimens with a Cambridge Stereoscan at 15 kV.

The material of *Linograptus posthumus* (Rheinhard RICHTER) illustrated on Pl. 1 is housed at the Institute of Palaeobiology of the Polish Academy of Sciences, Warszawa, and designated in the collection as ZPAL. G.XX.

THE FOSSIL RECORD

The recent views on the origin and evolution of linograptids owe much to the penetrating work of JAEGER (1959, 1960, 1969) as well as to papers by TELLER (1962, 1964) and PALMER (1971). I (URBANEK 1963) also contributed in a study based on well-preserved, isolated material from deep boring. It has elucidated a number of open problems concerning the linograptid phylogeny and astogeny. The descent of the linograptid lineage is a difficult problem. The crucial fact for its understanding is a striking resemblance between the early





Resemblance of the sicular part of rhabdosome as evidence of common ancestry. A, Pristiograptus dubius (SUESS, 1851). B, Lobograptus? sherrardae (SHERWIN, 1974). C, Neodiversograptus nilssoni (BARRANDE, 1850). D, Lobograptus progenitor URBANEK, 1966. All diagrammatical, growth lines in B are conjectural (after URBANEK 1966 and KOREN' and URBANEK 1994, modified). Abbreviations: dan – dorsal apertural notch of metasicula, dp – dorsal process of metasicula, ib – initial bud, msi – metasicula, psi – prosicula, r_1-r_6 – sicular rings (annuli), th_1-th_3 – successive thecae, v – virgula, vi – virgella.

representatives of the three major Ludlow lines of evolution - the Linograptinae, the Cucullograptinae, and the Neocucullograptinae (represented by Bohemograptus). Though these lines featured quite divergent trends of evolution, the differences between their early representatives were insignificant and did not increase until much later. This might suggest that all three derived immediately from a single ancestral species (URBANEK 1966, 1970). It was argued (URBANEK 1966) that this, still missing link must have resembled, in its essential features, Lobograptus progenitor URBANEK, 1966 - an early member of the cucullograptid lineage, and that it must have been devoid of either cucullograptid or linograptid specialization. KOREN' (1991, 1991a, and personal information) has most recently proposed Lobograptus? sherrardae (SHERWIN, 1974) from the praedeubeli Zone as the best candidate for their common ancestor and provided convincing stratigraphical and morphological evidence to corroborate her view. L.? sherrardae, which may be classified either as an advanced pristiograptid or a primitive linograptid, appeared due to adaptive radiation that followed the *lundgreni* Event, a great biotic crisis in the late Wenlock (KOREN' and URBANEK 1994). The material collected by KOREN' (1992) makes it possible to trace its origin to non-specialized survivors, namely to the Pristiograptus dubius stem lineage. In the praedeubeli Zone the divergence attained was still rather insignificant and consequently L.? sherrardae displayed only a slight distinction from its ancestor (cf. Fig. 1A, B). Such minor features as a gracilized and slightly dorsally curved proximal end of the rhabdosome, combined with some increase in the width of the sicular aperture, exhausted the linograptid "specialization" at that stage! Indeed, the crucial feature of the linograptid adaptive type - the ability to form sicular cladia - had not evolved yet, and the scope of future morphological (and ecological) changes remained wholly unpredictable at the L.? sherrardae stage of the evolution. Nevertheless, its morphology is unique among its collateral relations (described by JAEGER 1991 and KOREN' 1992), placing L.? sherrardae





Neodiversograptus nilssoni (BARRANDE, 1850) from N. nilssoni Zone, an example of the early linograptid organization. A_1 , proximal end of a young unipolar colony. A_2 , A_3 , an early and advanced growth stage of bilobate dorsal process seen in both aspects. Note the presence of asymmetric dorsal spine (ds) in $A_1-A_3 - a$ crucial linograptid specialization. A_4 , proximal end of the young primary cladium with growing theca 1^1 and sicula lacking any apertural elaborations. **B**, a young bipolar colony.

as an almost perfect candidate for a common ancestor of true linograptids (*Neodiversograptus nilssoni*) and the earliest cucullograptids (*Lobograptus progenitor*). Both the last named species share a number of common features with *L*.? *sherrardae* (as can be seen in Fig. 1A–D), and appear in stratigraphic sequence. *L*.? *sherrardae* represents the prelinograptid stage of evolution. Its obvious relation to the conservative pristio-graptids of the *dubius* group makes the earlier views on the cyrtograptid ancestry of linograptids entirely obsolete.

The prelinograptid stage of evolution is represented by *Neodiversograptus* with its two species recognized. The earlier of the two, *N. nilssoni* (BARRANDE) as defined by me (URBANEK 1954, 1963), occurs

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Advanced linograptid organization as revealed by: A, Neodiversograptus cf. beklemishevi (sample A, L. parascanicus Zone) exhibiting transitional features between N. nilssoni and N. beklemishevi, namely gracilized but holoperipheral theca 1². B, Neodiversograptus beklemishevi URBANEK, 1963 (from scanicus Zone), showing meroperipheral theca 1² and free virgella. C, Neodiversograptus beklemishevi (from leintwardinensis Zone) displaying slight deviation of virgella (vi) (B, C after URBANEK 1963, A after unpublished drawing by A. KOZŁOWSKA-DAWIDZIUK).

within the eponymous Zone. The sporadic occurrence of bipolar rhabdosomes in the populations of N. nilssoni, e.g. rhabdosomes composed of a primary stipe, a procladium and an additional sicular stadium (Fig. 2A, B), may be considered the first distinct manifestation of the linograptid trend of specialization (JAEGER 1959; URBANEK 1963). The sicular cladium is supported by a peculiar asymmetrically placed dorsal apertural spine of the metasicula (URBANEK 1954), which later forms an additional virgula of a kind, the pseudovirgula, of this cladium. This function of the assymmetric dorsal spine was accurately guessed by JAEGER (1959) although he had no direct evidence to support his supposition. The first such evidence was provided somewhat later (URBANEK 1963), and since that time more specimens of this kind have been found. The scarcity of bipolar rhabdosomes is indicative of a morphogenetically non-stabilized nature of the newly acquired trait whilst the robust appearance of the initial thecae in the sicular cladium suggests that there was a considerable lag in the generation of the cladium as compared with that of the primary stipe. Therefore the growth of the sicular cladium coincided with that of the distal thecae of the procladium. It is safe to conclude that those bipolar, "diversograptid" rhabdosomes had low frequency in the N. nilssoni populations but cooccurred steadily with the standard "monograptid" morph within the same breeding community.

The second species, N. beklemishevi URBA-NEK, 1963, occurs somewhat higher, namely in the interval between the L. parascanicus Zone (= the early part of the *L. scanicus* Zone) and the S. leintwardinensis Zone, as currently defined. It represents a more advanced stage of morphological evolution towards Linograptus, the pseudovirgula of the first sicular cladium being first formed as a symmetrically placed dorsal apertural spine. Moreover, the material available comprises both the forms which are capable of forming only one sicular cladium (Fig. 3A, unpublished material) and those having a potential ability to generate more such cladia (Fig. 3B). In the latter case, the first theca of the sicular cladium conceals

no more than part of the metasicular aperture, leaving considerable space to be used subsequently by additional sicular cladia. But even then the pseudovirgula stretches straight and forward, without producing any divergence (the angle between the dorsal wall of the metasicula and the theca is approximately 180° (Fig. 3C). It is only in the *S. leintwardinensis* Zone that the first occurrence of forms with a certain divergence was noted (an angle about 150°) (Fig. 4A). Such forms approach *Linograptus* to a great extent, except for the standard structure of their virgella.



Linograptus with its species L. posthumus (Reinhard RICHTER, 1875) attain a truly multiramous condition, all colonies being capable of forming more than one sicular cladium. The dorsal spine of the metasicula and, consequently, the pseudovirgula of the first sicular cladium usually diverges at an almost right angle from the aperture of the metasicula (Fig. 4B), thus leaving more space for the buds of additional sicular cladia which appear in a rapid succession (Fig. 5). They come out as small tubercules on the apertural margin of the metasicula that later extends into the pseudovirgula or the axis of a given sicular cladium. The first sicular cladium appears very early, with only a slight delay in respect of the primary stipe (procladium, Fig. 5). Up to 6 uniserial stipes are usually formed, but in some cases as many as 15 have been observed (JAEGER 1964). The four-stiped (JAEGER 1959, 1969) or six-stiped (TELLER 1964) rhabdosomes were claimed to represent the astogenetic norm (a fully grown typical rhabdosome). Although the data on the numerical prevalence of rhabdosomes consisting of a certain number of stipes at different stratigraphical levels are somewhat confusing (JAEGER 1969), the entirety of the evidence available points to the four-stiped compound rhabdosome as the basic morphological unit in *Linograptus*. Moreover, the intrinsic tetrameric arrangement of the *Linograptus* colonies is indicated by the symmetry



Fig. 5

Growth correlations within sicular part of the rhabdosome in *Linograptus posthumus* (Reinhard RICHTER, 1875). A-C, early stages showing concommitant growth of distal part of theca 1¹ and incipient portion of 1². D, Advanced stage showing that growth of theca 1¹ is completed simultaneously with the formation of prothecal part of theca 1² (after URBANEK 1963).

of the virgellarium, the termination of the long and robust virgella. This unique colonial device is composed of a membraneous portion (m) which produces four petals, each ending in a long fingerlike outgrowth (Fig. 5; Pl. 1: 1a, Vg, f).

The time of the appearance of the virgellarium cannot be precisely defined. The earliest finding of this structure, already fully developed, was recorded in the Mielnik borecore at a depth of 823.00 m and may be related to the *latilobus/balticus* Zone (for its definition see URBANEK 1995 and this volume p. 94). But the bulk of the linograptid material was obtained from somewhat earlier strata (837.60–820.00 m), that is from the *N. kozlowskii–Pseud. latilobus* Interzone. These linograptids, hardly differing from the later Přidoli forms, were probably provided with a virgellarium, which, however, has not been preserved. This assumption was recently confirmed by ŠTORCH (1995) who recorded *Linograptus posthumus* with typical virgellaria in the *kozlowskii* Zone of the Barrandian area. According to him these specimens are early representatives of the type subspecies (*L. p. posthumus*), although they reveal some features which fits better the earlier *L. p. tenuis*. Thus the early Ludfordian most probably corresponds to the time of the



Fig. 6

Pattern of colony organization in *Abiesgraptus* as interpreted by JAEGER (1959). The paired lateral cladia (L'₁-L₁) are produced at rather regular intervals only on the procladium (1) and on the first sicular cladium (2), while remaining two sicular cladia do not display branching (3, 4). S means sicula (after JAEGER 1959, modified).

origin of the virgellarium. The questions whether it could have appeared still earlier (in the *leintwardinensis* Zone) and whether its mode of appearance was rapid or gradual remain open. The appearance of the virgellarium and the multibrachiate nature of the compound rhabdosome are the main evolutionary novelties developed by *Linograptus*. It was capable of producing truly giant rhabdosomes with stipes more than 60 cm long and colonies numbering more than 1500 individuals (JAEGER 1969)! The stratigraphical occurrence of *Linograptus* is largely defined by the conventionally set morphological boundaries. For the purpose of the present analysis, its first appearance may be identified as the top of the *leintwardinensis* Zone whilst its upper limit is the top of *hercynicus* Zone.

In the Lower Devonian (the M. uniformis-M. praehercynicus Zone), the linograptids with a tetrameric foundation gave rise to highly symmetric (rhombic) colonies of Abiesgraptus (JAEGER 1959, 1969). As interpreted by JAEGER (1959), the Abiesgraptus rhabdosome is composed of two main stipes (the procladium and the first sicular cladium) producing, at certain intervals, paired thecal cladia, and of two additional sicular cladia placed normal to the main stipes and devoid of thecal cladia (Fig. 6). During its early astogeny, the Abiesgraptus rhabdosome is indistinguishable from the four-stiped Linograptus. It is not until later that many paired thecal cladia are produced on the two earliest stipes, which results in a sharp morphological discontinuity between otherwise closely related taxa. Thecal cladia grow bilaterally from the aperture of the parent theca (supra-apertural budding), being supported by a pseudovirgula, a rigid rod which probably emerged as a lateral apertural spine of the parent theca. The generation of paired thecal cladia on the main stipes of the Abiesgraptus rhabdosome may have led to an improvement of the colony balance and to a better use of space and food resources (JAEGER 1969). The resulting complex colonies densely covered large areas (approximately 1770 square centimetres), intensively exploited by a great number of zooids (perhaps more than 3000 zooids in a single colony; MULLER 1965). The presence of a virgellarium has not been proved in Abiesgraptus because of the strong "carbonization" of the central portion of the colony, making structural details quite obscure (JAEGER, personal communication). It is, however, equally possible that a virgellarium was present as a legacy from the linograptid ancestors or that it was already reduced to be replaced by a generally more efficient suspension system thanks to the

lateral branching and the extensive area occupied by the colony. The abiesgraptid species constituted the final stage of the *L*.? *sherrardae–N. nilssoni* evolutionary line, representing at the same time, one of the most complex graptoloid colonies ever formed. One can conclude that there are sufficient data allowing the origin, divergence and anagenetic advance in this lineage to be traced over an imposing time span – from the *praedeubeli* Zone (Homerian) to the *hercynicus* Zone (Lochkovian), and possibly even higher up to the *fanicus* Zone of Pragian, where last abiesgraptids were recorded.

While the bulk of the material available is strongly suggestive of a stepwise emergence of multiramous condition, the recent study by RICKARDS et al. (1994) on the Ludlow graptolite fauna from New South Wales (Australia), speaks in favour of a rapid origin of multiramous forms, directly from N. nilssoni. This is indicated by the occurence of an endemic multiramous form, Linograptus orangensis, at the bottom of the nilssoni Zone. The form in question is in some respects rather unique and even in opinion of RICKARDS et al. (1994: p. 12) "does not help understanding of the relationship of Neodiversograptus to Linograptus". This is because of the growth direction of sicular cladia in "L." orangensis are either reclined or straighforward (and only in one specimen a sicular cladium grows downwards). In my opinion the Australian form represents a stage of evolution comparable with N. beklemishevi and probably is of a somewhat later age (boundary of nilssoni-progenitor or even bottom of scanicus Zone). It is possible that large part of what is considered there the nilssoni Zone, should be already assigned to the scanicus Band, as it is indicated by the FA's of advanced lobograptids in NSW sections. The precocious origin of this multiramous form might be explained as illusory, an effect of different interpretation of stratigraphic data in Australia and in Europe. More enigmatic is the still earlier occurrence of a single specimen of multiramous Linograptus sp. in ludensis Zone. However, until more data are available I would prefer a stepwise emergence of *Linograptus*, to RICKARDS' hypothesis of its instantaneous origin from N. nilssoni. The latter view fails to explain why in Europe the evolution of multiramous linograptids is stretched over several graptolite Zones.

THE FUNCTIONAL AND ADAPTIVE MEANING OF THE EVOLUTIONARY CHANGES

The life orientation of the standard monograptid uniramous colony in the water column has not been convincingly established, current opinions representing contradictory views summarized in the papers by BATES and KIRK (1984), LENZ and CHEN (1985), and FINNEY and JACOBSON (1985).

In the light of new studies (RIGBY and RICKARDS 1989; RIGBY 1992) on physical models of graptoloid colonies, the characteristic dorso-ventral curvature in the proximal part of the *N. nilssoni* procladium could be regarded as a factor causing the rotation around the long axis and enhancing the feeding efficiency. There is little doubt that the appearance of two-branched, bipolar-growing ("diversogratid") rhabdosomes in *Neodiversograptus nilssoni* had a great impact on the balance and hydrodynamic properties of the colony. The resuling situation, however, can only be described in a hypothetical way.

Accepting the vertical orientation of the uniaxiate monograptid colonies as the most reasonable hypothesis, one could posit a horizontal orientation for the diversograptid bipolar morphs. This may be visualized all the more easily assuming a heterodoxal, "upside down" life orientation of monograptid colonies, with the sicula directed upwards as suggested by KIRK (1969, 1972, 1978). The change of orientation from the standard form to the diversopraptid one may be expressed as follows: $\overline{V} \rightarrow H-$, where \overline{V} is vertical orientation with the sicula directed upwards, whilst H-denotes a horizontal life position with the sicula in the middle (Fig. 7A, B).

Less obvious is the impact of such changes on the balance of the uniaxate colonies oriented vertically with their siculae positioned downwards (\underline{V} , Fig. 7A). It seems probable that in the latter case the bipolar rhabdosome preserved its primary vertical orientation: $\underline{V} \rightarrow V-$, rather than changing it to a horizontal position: $\underline{V} \rightarrow H-$ (Fig. 7C).

A reversed orientation as proposed by KIRK (1969) would be a kind of prospective adaptation to future changes in the life position of the rhabdosome. Such horizontally oriented bipolar rhabdosomes, both in their rectilinear and bent form, ought to face a number of hydrodynamic problems, even if one assumes fairly great flexibility during life.



Fig. 7

Diagram showing the possible orientation of linograptid colonies in the water column: A, B, vertical orientation of unipolar colony with its sicula downwards (A) and upwards (B); C_1 , C_2 , possible orientations of siculate bipolar colonies, with sicular cladium downwards (C_1) or both cladia oriented horizontally C_2); D, compound colony of *Linograptus* oriented with virgellarium (vg) and sicula upwards while proximal part of branches are pendent and later bent subhorizontally. Further explanations in text.

The ability to generate a number of sicular cladia in *N. beklemishevi* was a certain improvement in the stability of the rhabdosome and produced a larger working surface which may have prevented sinking. But it was the appearance of a regularly multiramous *Linograptus* rhabdosome that radically improved the balance of the colony, ensuring a far better stability in calm waters. The presence of a divergence angle in the proximal portion of the stipes resulted most probably in a pendent position of the rhabdosome (\overline{P}) , at least in the early astogenetic stage (URBANEK 1963). This may take the form of: $H^- \rightarrow P$ and is shown in Fig. 7D as seen in the isolated proximal fragments of some such rhabdosomes.

However, the distal portions of the cladia were secondarily reflexed taking again a more horizontal orientation (JAEGER 1959). Thus the orientation of the *Linograptus* colony may be described as changing astogenetically from pendent (\overline{P}) in the centre to horizontal (H–) or subhorizontal (SH–) on the periphery. As long as we assume a buoyancy function of virgellarium (vg), a reverse position of rhabdosome (with vg oriented downward) seems very unlikely.

Such distinct differences in the shape of particular growth stages of the colony provide evidence of their obviously different mode of life position in the water column, and general hydrodynamic properties.

According to FINNEY (1986), such growth differences were instrumental in avoiding too severe intraspecific competition thanks to confining the juvenile and the mature growth stages to different habitats. This strategy was surely important for organisms like linograptids which probably frequently lived in huge and densely crowded populations.

A Linograptus colony may be visualized as essentially passively suspended in the water column due to a specialized device, the virgellarium (cf. p. 240). Its structure and position within the rhabdosome is strongly suggestive of a buoyancy function (URBANEK 1963; TELLER 1964; JAEGER 1969) although its operation is difficult to understand. The earlier suggestions that the virgellarium was merely part of the skeleton supporting a vesicular structure made of soft tissues (URBANEK 1963) are undermined by more recent views on the mode of secretion of the graptolite colonies. (CROWTHER 1981). They assume a purely pterobranch way of secretion by individual contributions of the zooids, which depositing new skeletal material due to the movements of the cephalic disc were responsible for the secretion of both the fuselli and the cortical bandages (see URBANEK 1986 for an extended discussion of this question). The presence of any extrathecal soft tissue in graptoloid colonies seems therefore doubtful, although FINNEY (1979) presented new and suggestive data in favour of the old idea about the presence in them of vesicular buoyancy organs. Still it is also possible that the petals and the finger-like outgrowth of the virgellarium served as the place of attachment of a gas bubble or a large droplet of a liquid fatty substance capable of reducing the relative density of the colony (Fig. 5). Such a buoyancy material may be imagined as secreted by the siculozooid, and regulation of its amount could result in vertical migration of the colonies. In the Early Přidoli, several branches within a single linograptid colony produced an additional suspension effect (although they mostly served as stabilizers), while geologically younger forms with a reduced number of branches were suspended mainly with the help of an elaborated virgellarium (Fig. 7D, vg).

The generation of lateral thecal cladia in addition to the main stipes of the *Linograptus* rhabdosome finally solved the problem of balance. The resulting *Abiesgraptus* compound colony was strongly stabilized. The potential ability to produce lateral thecal cladia appeared early in the phylogeny of the *Linograptus–Abiesgraptus* line of descent, as shown by the sporadic occurence of rhabdosomes provided with only one pair of thecal cladia (TELLER 1964; the Přidoli, probably the *ultimus* Zone) or even with a single unilateral cladium (JAEGER 1969; the Lochkovian, the *uniformis* Zone). Such trials which instantly offered a certain advantage in the balance were probably favoured by natural selection and followed by a more ordered generation of numerous thecal cladia with a precise morphogenetic control of their formation (see p. 256 herein).

In addition to a high degree of stability, lateral thecal cladia also accounted for an increase of the working surface in *Abiesgraptus*, which prevented sinking and had a suspension effect. Combined with the flattening of the proximal part of the rhabdosome, these features made the *Abiesgraptus* colony leaf-like.

This suggests that advanced linograptids were partly hydrogliders capable of gliding on horizontal currents (BERRY *et al.* 1987). However, in contrast to what BATES and KIRK (1984) say they were not stiffly branching, but highly flexible, yielding to wave motion rather than resisting it.

This rhabdosome type seems to represent extreme adaptation to the near surface dwelling. Thus the entire evolution of linograptids may be interpreted as an escape from the oxygen deficient zones towards better aerated surface waters, with Abiesgraptus manifesting the terminal stage of the process. The above interpretation differs from that of BATES and KIRK (1984) who posit that Linograptus and Abiesgraptus were lower layer colonists (a habitat created, in their opinion, in the Late Silurian-Early Devonian as a result of eustatic changes in the sea level!) and not surface dwellers. The present interpretation seems to offer a better explanation of the foliate shape of the Abiesgraptus rhabdosome, agreing well with the most recent model of the hydrochemical regime of the Silurian seas proposed by BERRY et al. (1987). Based on the Recent conditions observed in the Pacific Ocean off Peru, this model assumes the presence of a "hanging", shallow (a few hundred meters deep) Oxygen Minimum Zone (OMZ) instead of a massive bottom anaerobic zone as implied by the classical Black Sea model. The upper level of the sea must have constituted the graptoloid habitat while the presence, depth and thickness of the OMZ were probably the main environmental factors controlling their evolution. Moreover, linograptids (and especially L. posthumus) were ubiquitous representing an almost omnipresent element of the various graptoloid assemblages. According to the line of reasoning offered by COOPER et al. (1991), such behaviour seems more indicative of an epipelagic depth zone than of any deep water biotope. Therefore, unlike the slender multiramous Ordovician dichograptids and contrary to what was posited by BATES and KIRK (1984), linograptids must have occupied the near surface waters of the ocean, "leaking" from this biotope into the epipelagic zone of the shelf.

The pattern of the *Abiesgraptus* rhabdosome,especially its numerous and regularly spaced lateral cladia, indicates that a certain principle of economy was involved in the formation of such colonies (JAEGER 1959). *Abiesgraptus* evidently represented an instance of a very effective utilization of space and exploitation of the trophic resources. FORTEY and BELL (1987) applied the notion of harvesting array for graptoloid colonies, considering this factor to be responsible for the pattern of the multiramous ones. Linograptids provide a convincing example of the maximization of harvesting efficiency. As calculated by MÜLLER (1965), an *Abiesgraptus* colony covered an area of some 170 square cm exploited by more than 3000 zooids on its branches! Thus a high harvesting efficiency was achieved in *Abiesgraptus* through a mere increase of the number and concentration of zooids (dense packing in a limited area). The solution of the adaptive problem, however, did not involve the elaboration of complex apertural aparatuses allowing an increase in the individual feeding efficiency of particular zooids (the trend of recorded evolution encountered in the Cucullograptinae and Neocucullograptinae and a number of other groups). The strategy chosen by the linograptids resulted in the development of simple thecae and complex colonies whereas in the majority of monograptids the thecae were elaborated and the colonies simple.

Thus the flat leaf-like colonies of *Abiesgraptus* featured an adaptive syndrome ensuring the solution of the three main problems at once: a perfect balance of the colony, its almost steady suspension, and a high harvesting efficiency of the colony as a whole.

A MORPHOGENETIC INTERPRETATION OF THE RECORD

The appearance of a bipolar siculate morph in *Neodiversograptus nilssoni*, although *per se* a crucial evolutionary event, was by no means unique. Sporadic occurrences of such bipolar rhabdosomes were recognized by RICKARDS (1973) and RICKARDS *et al.* (1977) in a number of quite unrelated monograptid groups. It may be thought, therefore, that the latent ability to produce sicular cladium in advanced astogenetic stage, was a common feature in most monograptids. Phenotypic expression of this morphogenetic potential in *N. nilssoni* (and in other similar cases), may probably be ascribed to developmental switches, due to mutation or other changes in the genomic background, as it was recognized in epigenetic systems of many extant organisms. In the case of *Diversograptus* and *Neodiversograptus* this new pattern of development was later fixed as a norm, probably due to favourable selection pressure. The nature of the adaptive advantage represented by bipolar morph is obscure and may only be hypothetized (see p. 242, herein), but the evolutionary success of it is clearly demonstrated by the available fossil record.

Moreover, the ability of *Neodiversograptus nilssoni* to generate not only a normal monograptid branch (the procladium), but also an additional one (the sicular cladium) seems to be due to a mechanism similar to the rejuvenation of the siculozooid. The daughter individual (1^2) produced by the siculozooid (si) conceals the entire metasicular aperture, leaving no space for the siculozooid proper (Fig. 2B). Therefore the first zooid of the sicular cladium (1^2) may only be considered a further growth stage of the metasiculozooid, the result of additional growth after a considerable arrest marked by the thickened apertural margin of the metasicula. This may be best explained as a morphogenetic reactivation of the metasiculozooid, a process similar to the cases of rejuvenation or parricidal budding in some corals. After being rejuvenated, 1^2 generated 2^2 , the first zooid proper of the sicular cladium.

The asymmetric position of the dorsal apertural spine (ds) of the metasicula, later transformed into the pseudovirgula of the only sicular cladium and shifted secondarily into the plane of symmetry, corroborates the view that the entire construction was relatively imperfect at the early stages of its phylogeny. This asymmetry, in turn, was a direct effect of the bilobate nature of the dorsal process divided by a notch into two lateral lobes (URBANEK 1954; Fig. 2A₂, A₃ herein). Thus, the above-mentioned relative imperfection resulted from simple topographic or geometrical constraints.

The large size of its thecae suggests that the sicular cladium in *Neodiversograptus nilssoni* was a later formation than the primary branch (the procladium). From the growth correlation control within the graptoloid colonies it follows that isochronous thecae are isomorphic (Thorsteinsson rule, URBANEK 1960, 1963, 1970). Thus, the size and shape of the first thecae of the sicular cladium in *N. nilssoni* are indicative of their being formed simultaneously with the distal portion of the procladium (the primary stipe). The rich material analysed by PALMER (1971) shows that the sicular cladium was usually formed around the theca 16^1 growth stage of the procladium, although a certain lag in the development of theca 1^2 observed

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in other multiramous monograptids may account for its somewhat earlier initiation (say at the theca 13¹ stage). A considerable variation in the timing of the appearance of the sicular cladium has also been demonstrated.

Because of the large size of theca 1^2 , its base filled the entire space of the metasicular aperture, which instance may be termed the holoperipheral budding (Fig. 8A). As a result, the aperture of the sicula was completely sealed; there was no space for more buds initiating additional sicular cladia. This was a new geometrical constraint, allowing the formation of only a single sicular cladium. Moreover, the big size of the growing 1^2 involved the incorporation of the main portion of the virgella into the ventral wall of the growing theca, thus excluding the possibility of a progressive modification of the virgella, so characteristic of the later history of the Linograptinae (Fig. 2B, vi).

The majority of *N. nilssoni* specimens figured by PALMER (1971) display some degree of divergence of the sicular cladium, the result of a similar divergence in the growth of a long (up to 8 mm) and stout dorsal apertural spine of the metasicula, which later transformed into the pseudovirgula of the sicular cladium. This contrasts with the straightforward growth of this spine in *N. beklemishevi*. However in *N. nilssoni*, the generally robust theca 1^2 conceals the entire apertural margin of the metasicula (PALMER 1971; Fig. 4 therein), thus the divergence of branches has no effect on making more space for additional sicular buds. Later, after the gracilization of theca 1^2 , such divergence produced a far-reaching result, namely, meroperipheral budding (see p. 248 herein).

A delay in the generation of the sicular cladium in *Neodiversograptus nilssoni* accounts for the fact that not until the 16¹ thecal stage was it able to attain the bipolar, diversograptid organization. Although the presence of the long dorsal apertural spine of the metasicula, a prerequisite for the formation of the sicular cladium, is a species-specific character, only a fraction of the colonies displayed the bipolar phenotype. Was the appearance of the bi-ramous rhabdosome only a function of the age of the colony, or did it also involve some genetic differences? The answer is naturally uncertain (see p. 247 herein). But it is worth mentioning that the genetic factors which control the formation of the cladium were expressed fairly late in the astogeny of the *Neodiversograptus nilssoni* colonies.

The populations from the *parascanicus-scanicus* Zone which may be assigned to *Neodiversograptus* cf. beklemishevi are composed of forms invariably provided with a symmetrically placed dorsal apertural spine of the metasicula. In spite of this change, these populations still comprise both forms displaying the holoperipheral budding of theca 1² and therefore capable of forming only one sicular cladium (unpublished MSc thesis of A. KOZŁOWSKA-DAWIDZIUK), and much more advanced forms. The latter morph features a much smaller size of theca 1^2 , thus leaving part of the sicular aperture uncovered and creating a potential for the formation of more than one sicular cladium. This situation may be termed the meroperipheral budding as only part of the aperture of the mother theca is being used (Fig. 8C). In accordance with the Thorsteinsson rule (see p. 245), the smaller size of theca 1^2 is indicative of its earlier generation, at a time coinciding with the growth of the proximal thecae. It is obvious therefore that the mechanism of astogenetic acceleration was used to avoid the obstacles resulting from the above-mentioned geometrical constraints. At the same time, the virgella was set free from its association with the ventral wall of the bulky holoperipheral 1², entering the path of its future modification. These comparative advantages were still combined with certain imperfections, such as the straightforward growth of theca 1^2 , a mechanical consequence of the same direction of the symmetrical dorsal apertural spine of the sicula, extending into the pseudovirgula of the cladium (Fig. 3A, B).

Thus the course of phylogenetic events was not quite consistent. An earlier trait – the ability of the dorsal apertural spine of the metasicula to diverge, so frequent in the early *N. nilssoni* populations (PALMER 1971), was somehow lost and replaced by a potentially less adaptive ("inadaptive") character state, namely the straightforward orientation of the above spine in *N. beklemishevi* (URBANEK 1963). The adaptive inconsistencies of the real course of the evolution are demonstrated by (1) the functional ineffectiveness of the divergence of the two stipes because of the bulky size of 1^2 in *N. nilssoni* which, in spite of the divergence, covers the entire metasicular aperture, (2) the dissapearance of the divergence when the gracilized theca 1^2 makes it possible to free a part of the apertural space for the additional buds, and moreover, (3) the later restitution of the divergence in the linograptid stage of evolution, thus producing secondarily the most adaptive combination (small theca 1^2 plus the divergence of the sicular cladium (see p. 247 herein). Such a zig-zag pattern of behaviour of a single character seems not exceptional in the phylogeny.

The meroperipheral mode of budding in the advanced forms of *Neodiversograptus beklemishevi* resulted in the co-existence of a physiologically active metasiculozooid (si) with its daughter individual





Geometrical constraints at the aperture of metasicula (si) in Linograptinae: A, holoperipheral budding of theca 1^2 in *Neodiversograptus*, occupying the entire diameter (d) of metasicular aperture and leaving no free space for additional buds. This situation produces an obstacle for generation of more cladia. B, more free space (d₂, Si₂) may potentially be gained by simple widening of the aperture from diameter (d₁, Si₁). A free space created in this way could be used by additional cladia. C, free space at the sicular aperture (arrow) may also be attained by slimming of theca 1^2 (change from diameter d₁ to d₂), which needs an accelaration in formation of theca 1^2 , because of growth correlation within the colony. D, more free space at the sicular aperture may be attained with the same width of 1^2 , through a deviation in the direction of its growth. Free area is directly related to the angle of deviation, α .

 (1^2) . The latter is no longer a rejuvenated or parricidal siculozooid, but a normal blastozooid formed due to budding from its parental individual which, correspondingly, behaves as 2^2 in *N. nilssoni*. This effect may also be interpreted as a result of acceleration (see Figs 2B and 3B).

The emergence of *Linograptus* was therefore intimately related to the generation of a number of cladia from the aperture of the parental metasicula, which posed a constructional problem — an elegant and simple instance of constraint. In the case of linograptids, the nature of the constraint is both developmental and physical, as the realization of the multiramous pattern of the colony (a certain phenotype!) is prevented by the physical (geometrical) properties of the metasicula, that is by the limited space of its aperture (Fig. 8A). This hindering of the formation of additional buds imposes quite severe boundary conditions on the development of a multiramous rhabdosome. However, such constraint, arising from the local topographic situation, might be overcome, at least potentially, by a number of simple solutions, e.g. (1) by the expansion (widening) of the aperture of the sicula (Fig. 8B), (2) by the narrowing of the base of the daughter theca 1^2 (Fig. 8C) and leaving in this way some free space, or (3) by the divergence of the primary sicular cladium due to a change in the direction of its growth, thus creating free space for additional buds (Fig. 8D). It is quite obvious that each of these changes (1-3) would have produced some open space at the sicular aperture which could have been used by a number of additional buds, each initiating a new sicular cladium. However, in the real course of evolution, linograptids never used solution 1, although monograptids with a strongly expanded (trumpet-like) sicula occur sporadically in the Upper Silurian and are common in the Lower Devonian. What they used instead was a combination of solutions 2 and 3 (Fig. 8C, D). As a result, theca 1² is both slimmer and diverging. The primary requirement getting slimmer - was in itself quite a complex task because of another developmental constraint - the regulatory mechanism controlling the size and shape of the thecae which are generated simultaneously on the growing tips of the multiramous colonies. Thus a lag in the formation of theca 1², the primary cladium, resulted in its concommitant growth with one of the distal thecae (usually 16^1 or even a more distal one) and, correspondingly, determined its robust appearance [the above Thorsteinsson rule (p. 245) stating that isochronous thecae are isomorphic because of their equal morphogenetic potential]. Large-sized 1^2 thus appeared due to holoperipheral budding as defined above. The change to a meroperipheral condition involved the acceleration of the generation time of 1² in order to make it grow simultaneously with a much more proximal theca (approximately with 2^{1}), which automatically dictated its smaller size (Fig. 8C). In other words, formation of 1^2 in L. posthumus is accelarated by 15 thecae as compared with N. nilssoni.

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Thus the processes involved are much more than mere diminution of the thecae of the first sicular cladium – they followed a rigid pattern of colony organization with its system of growth correlation.

The second elementary process, consisting in the divergence of the sicular cladium (change in the growth direction), is of particular importance for it produces more free space for a given diameter of the base of 1² (Fig. 8D). As suggested by URBANEK (1989), the problem of the geometrical constraint can be quantified in a simple way. The angle of divergence (marked D or B) is related to the angle of deviation of theca 1² according to the formula: $\beta = 180^{\circ}-\alpha$ and $\alpha = 180^{\circ}-\beta$.

The free space created by the moving away of theca 1^2 is proportional to D-x, where D is the diameter of the sicular aperture and x = d cos α . Therefore the space (area) which may be operationally used by the additional buds is directly proportional to the angle α , attaining its maximum at $\alpha = 90^{\circ}$ (cos $90^{\circ}= 0$ and correspondingly x = 0 whilst the free area equals that of the entire aperture!), but inversely proportional to the diameter of the base of 1^2 . The area accessible to the additional buds is proportional to the free surface of the aperture and may be calculated from the formula given below. The area of the sicular aperture, A, could be aproximately calculated by considering it a circle with a diameter D, which equals that of the aperture, in other words by using the formula: $A = 1/4 \pi D^2$.

In holoperipheral budding (e.g. in *Neodiversograptus nilssoni*), the diameter d of the circular base of theca 1^2 is equal to the diameter of the sicular aperture, D, (d = D). The sicular aperture is completely concealed by the circular base of theca 1^2 (the concealed area C = A) and naturally there is no free space F left, thus F = 0.

Advanced linograptids with the meroperipheral budding of theca 1^2 display, however, a different relation, D > d, and in their case, the base of theca 1^2 conceals only a portion of the apertural area (C), leaving the rest of it (F) free: A-C = F, where A and C are the areas of the bigger circle (the sicular aperture) and the smaller one (the base of theca 1^2) as shown in Fig. 9.

Additional free space may be created by the turn of the base of theca 1^2 by an angle α contained between the plane of the sicular aperture and that of the base of theca 1^2 as can be seen in Fig. 8D. The angle α , showing the deviation of theca 1^2 from its horizontal position, is related to the commonly measured angle of divergence of the two main branches of the rhabdosome, β ; thus $\beta = 180^{\circ}-\alpha$. As a rough approximation, one can assume that the recondite area of the sicular aperture corresponds to the orthogonal projection of the base of theca 1^2 on the plane of that aperture. Such a projection represents an ellipse (Fig. 9), whose minor axis b may be calculated from the simple relations shown in Fig. 8D, namely b = d cos α , whilst its major axis, a, remains constant, a = d.

Therefore C, the area concealed by the deviating base of theca 1², is equal to the area of such an ellipse $(S = \pi ab)$ and may be calculated by the formula: $C = \pi d^2 \cos \alpha$. From the above it follows that C depends on the value of $\cos \alpha$ and varies inversely as α increases within the quadrant 0–90°. The greater the angle of the sicular cladium deviation, α , the larger the uncovered area produced within the aperture. At a given angle α , the uncovered area (F) of the sicular aperture equals A–C, where A and C may be calculated by the formulas defined above, and the free area is $F = 1/4\pi D^2 - \pi d^2 \cos \alpha$.

The above simplistic approach is valid under the condition that d is considerably smaller than D, d < D, which is certainly true in the case of meroperipheral budding, e.g. in *Linograptus*: $d \sim 1/3D$. Only then the entire concealed area fits within the limits of the aperture, A. But when both diameters are close to being equal, $d \sim D$, the recondite area falls largely outside the limits of A, making the calculation of the uncovered area a less trivial task!

This simple case of a single sicular cladium may easily be spread to embrace a multiramous condition involving m sicular cladia under the assumption (and a fairly realistic one) that α and d remain very similar for all branches. Thus a strongly reduced free area, F, will become: F = 1/4 πD^2 -m $\pi d^2 \cos \alpha$.

In extreme cases where m = 15, the bases of the sicular cladia were unbelievably tightly packed, the siculozooid being transformed into a sort of a stolonal node and a bunch of stolons radiating from the aperture of the sicula.

However, standard tetrameric *Linograptus* rhabdosomes offered more space for the continuation of the activity of the siculozooid along with that of its daughter zooids.

The divergence of the dorsal apertural spine of the metasicula (later transformed into the pseudovirgula of the sicular cladium) may be interpreted also as co-aptation — an instance of regulatory adjustment of different parts of the evolving biosystem in the course of evolutionary changes.

In the real phylogeny, the first process, the acceleration of the formation of 1^2 and its resulting gracilization, occurred earlier (*N*. cf. *beklemishevi*, the *scanicus* Zone) whereas the second one, the change in the direction of the growth of 1^2 , was triggered somewhat later (*Neodiversograptus/Linograptus*)



Fig. 9 Relation of coancealed area of metasicular aperture (strippled) from α, the angle of deviation of sicular cladium. Further explanations in text.

transients, the *leintwardinensis* Zone, attaining divergence angle, D_A of some 150° and α 30° as compared with D_A 115° and α 65° in typical *L. posthumus*). Secondarily, however, both features were fused into a single adaptive syndrome.

The *Linograptus* astogeny features a few other changes, which may also be interpreted in the light of the morphogenetic mechanism. The shortening of the metasicula, which is distinctly reduced as compared with that in *Neodiversograptus*, reveals a tendency towards rapid generation of cladia, the metasiculozooid being only a nodal point in the astogeny. A greater share of the prosicula (the larval theca), than that of the metasicula (the theca of a metamorphosed zooid), was interpreted as phoetalization of some kind (URBANEK 1963).

The *Abiesgraptus* rhabdosome appears through the generation of paired thecal cladia on the two primary cladia of the four-branched linograptid foundation. The distance between the mother thecae of the thecal cladia growing distalwards (MULLER 1965) is an example of morphological gradients in compound colonies. Each paired thecal cladium which budded from the aperture of a mother theca most probably created a morphogenetic field exerting control over a certain area of the main stipe and inhibiting the formation of other thecal cladia. The areas controlled in this way increased distalwards.

Morphological changes in the evolution of the Linograptinae were focused on the pattern of the rhabdosome, with only negligible effects in the thecal morphology. Whilst the thecae retained their simple structure with only some minor changes, the pattern of the rhabdosome was profoundly transformed. It was the entire colony rather than individual zooids that were the target of natural selection.

A POSSIBLE RECONSTRUCTION OF THE NUMERICAL DYNAMICS IN LINOGRAPTID CHRONODEMES

The temporal species (chronospecies) described within the Linograptinae (*N. nilssoni*, *N. beklemishevi*, *L. posthumus*, *A. tenuiramosus*) were recognized on the basis of a certain distinct morphological norm. One can assume that such norms can easily be traced in large samples, corresponding most probably to the periods of proliferation (acme) of a given lineage. Thus the discrimination of the temporal species is



Fig. 10

A diagram showing the alternating pattern of proliferation (A, C) and scarcity (B) of fossil populations (chronodemes) as revealed in the stratigraphic sequence and related to the evolutionary dynamics and variation spectrum of the populations within a lineage. The periods of abundance correspond to adaptive equilibrium when adaptive optimum (+) is situated close to the norm (N) and selection pressure has a stabilizing effect (S with equal arrows in A). During the periods of scarcity, primary norm (PN) and adaptive optimum (+) disjunct resulting in a directional selection (S with inequal arrows) and a gradual shift of the mean (B). Next adaptive equilibrium is attained when a new norm (NN) reaches the position of actual adaptive optimum (+) and stabilizing selection is restored (C). Most chronospecies are defined by populations like A and C.

to a large extent preconditioned by the very nature of the fossil record displaying episodes when the populations (chronodemes) show high abundance, alternating with intervals of relative scarcity.

Hence prolific populations are commonly discriminated as separate taxa, whilst the taxonomic evaluation of less abundant populations, which occur at the borderline between the adjacent, well-defined chronospecies (*nilssoni-beklemishevi-posthumus*), poses a difficult task. One can hypothesize that during such intervals the population size of successive chronodemes was reduced, thus producing a "bottleneck effect" and creating conditions for a faster transformation. Among such populations a morphological norm is difficult to define because of their scarcity, on the one hand, and considerable changes in the subsequent zonal populations (chronodemes), on the other. Such zonal variation makes any lumping of these populations into a clearly defined species a questionable procedure.

The above pattern of alternating proliferation and scarcity, or of a well-stabilized morphological norm and a changing one, as observed in the history of the Linograptinae, can be interpreted as follows (Fig. 10).

Prolific populations were probably associated with the periods of adaptive equilibrium, when selection pressure having a stabilizing effect was less severe. In terms of punctualism, these periods could be

described as stasis, although the application of this term does not imply the entire philosophy of this phenomenon as usually suggested by punctualists. Such periods of relative abundance and stabilized morphology were rather short in the case of *N. nilssoni* and *N. beklemishevi* and fairly long in such species as *L. posthumus* (Fig. 10A, C).

The intervals separating the periods of stasis featured a loss of adaptive equilibrium when there was a shift between the most adaptive condition (favoured by selection) and the previous norm, already fixed in the course of evolution. The resulting directional (dynamic) selection was probably a mover responsible for a relatively fast transformation of the population structure and the phenotypic expression of certain traits (Fig. 10B).

In the Linograptinae, the rate of morphological changes was, however, never particularly high. The presence of transient forms, although insufficient for tracing every change, suggests an essentially continuous pattern, but a succession of rapid shifts cannot be excluded. That is the reason why such scanty and variable populations set an uneasy task to a taxonomist and frequently are simply omitted in identification procedures. In the present paper, they are treated as a borderline between the parental and the daughter temporal species. The processes associated with those periods of relative instability may most probably be regarded as speciation events. As no branching (splitting of the lineage) occurs, such speciation should technically be defined as phyletic speciation or transformation.

The change from *L. posthumus* to *A. tenuiramosus* reveals a somewhat different mechanism – a slow transformation in large populations, without any evidence of bottlenecking in the lineage. Quite to the contrary, the fossil data demonstrate that immediately before the appearance of the descendant species, the ancestral *L. posthumus* displayed (at least in Central Europe) a genuine population explosion (see p. 256 herein).

Thus the periods of relative stability within the sequential species of the linograptid lineage cannot be understood as a complete arrest of morphological change. Such an arrest can be observed in some monophyletic lineages, e.g. *Gryphaea* (HALLAM, 1982) or *Metrarabdotos* (CHEETHAM, 1987). On the contrary, the "zonal evolution" in *Linograptus posthumus* may be used as an example of a series of changes (in the number of the sicular cladia, in the appearance of the thecal cladia or in the direction of the growth of the branches in the proximal end of the rhabdosome), which alone would not be sufficient for the discrimination of a morphospecies as currently defined, but which doubtlessly produce a cumulative effect influencing the course of the phylogeny.

AN ANALYSIS OF THE PERIODS OF STASIS WITHIN THE LINOGRAPTID LINEAGE

The populations (chronodemes) of *Neodiversograptus nilssoni* from the *nilssoni* Zone were composed of two distinct morphotypes: (1) the standard monograptid form with a uniramous rhabdosome and (2) the diversograptid form with a biramous (bipolar) rhabdosome. Although the latter morphotype is rare as compared with the standard one, it seems that the diversograptid form was a steady component of the *N. nilssoni* populations. One may conclude that in spite of the discontinuity of the phenotype, both morphs co-occured within a single breeding community and most probably were capable of intercrossing.

Essentially, the diversograptid morph is merely a more advanced (extended) astogenetic stage of the standard monograptid morph. Therefore its scarcity may be ascribed to the delayed expression of the colony's ability to generate a sicular cladium in the course of the astogeny. Few colonies survive long enough to be able to form one. Thus the age structure of the population and the rare occurrence of old colonies within a given population could be responsible for the scarcity of the bipolar phenotype. Yet it is rather certain that one could regard the monograptid and the diversograptid phenotypes as an instance of genetic polymorphism and their steady co-occurence as a result of balanced polymorphisms.

The relative numerical abundance of *N. beklemishevi* in the *scanicus* Zone most probably means the attaining of another adaptive equilibrium at a new stage of the morphological evolution represented by a novel morphological norm. The earlier formation of the sicular cladium as a result of an astogenetic acceleration (see p. 247 herein) led to an increase in the number of diversograptid morphs within each chronodeme, assuming that the age structure of the populations had not changed since *nilssoni*. The rhabdosomes which at the early stage of astogeny represented the juvenile, monograptid morph were later

A tentative scheme showing the range and trends in variation of *Linograptus posthumus* (Reinhard RICHTER, 1875) as revealed by number of cladia (procladium + sicular cladia, N) in populations from successive time-levels (T). 1–5 turning points in the phylogeny: 1–2 trend toward polybrachiate condition, 2–3 gradual decrease in the number of cladia until four-branched (tetrameric) condition is attained (3–4), being a structural foundation for compound colonies of *Abiesgraptus* (4–5). Changes in number of sicular cladia are associated with sporadic appearence of lateral (thecal) cladia as noted by asterisks (*). The taxonomic status of Lochkovian *Linograptus* is uncertain as it may represent juvenile colonies of *Abiesgraptus*. Based mainly on data from JAEGER 1959, 1969 and TELLER 1964.

replaced by more advanced diversograptid (bipolar) growth stages. An accelerated realization of the diversograptid rhabdosome may be ascribed to the action of selective forces favouring an earlier expression of the advantageous phenotype.

It is highly probable that some fraction of the *N. beklemishevi* rhabdosomes attained a multiramous stage, thus resembling and foreshadowing the pattern of the *Linograptus* colonies.

Linograptus posthumus, a representative of the genus in the Upper Silurian of Europe characteristically occurs in large populations, frequently displaying mass occurrences (as pointed by JAEGER 1959: p. 153,

"In Bereich grösster Häufigkeit werden viele Schichtflächen wie ein Teppich von den langen Zweigen bedeckt...").

This obviously is an indication of a great evolutionary success of the species and doubtless evidence of its adaptive equilibrium. The same is indicated by a wide geographic distribution of L. *posthumus* and the considerable duration of the species.

The occurence in large populations and a high perfection of adaptation resulted in the stabilization of the morphological norm, with only restricted evolutionary changes observed. These were expressed in minor changes of the width of the branches (*L. posthumus posthumus* and the subspecies *tenuis*) and possibly also in the certain zonal evolution of the number of cladia generated. Somewhat contradictory data (JAEGER 1954; TELLER 1964) were later summarized by JAEGER (1969, 1978) who posited directional evolution in a number of the cladia. The earlier populations are marked by a greater variation with a considerable share of multiramous colonies, sometimes exceeding 10 cladia (Ludfordian, Přidoli), whilst the later ones (Lochkovian) display a certain reduction of variation with a distinct predominance of tetraramous forms. The last named morphotype served as a morphological foundation for the origin of *Abiesgraptus* (Fig. 11).

The recognition of linograptid origin of *Abiesgraptus* and the reconstruction of the main stages of its astogeny we owe to the penetrating study by JAEGER (1959). *Abiesgraptus* appears for the first time in the *uniformis* Zone of Thuringia and dissappears in the *praehercynicus* Zone or in the lowermost portion of the *hercynicus* Zone (JAEGER 1954). However, LENZ (1988) found specialized abiesgraptids as high as Pragian of Arctic Canada (p. 261). Its previously restricted geographic distribution has recently been found equal to that in *Linograptus*, while the stratigraphic duration of the genus is much shorter. According to JAEGER (1959), *Abiesgraptus*, from its first appearance, featured a distinct and highly regular morphological pattern of the rhabdosome. Some differences in the width of branches, the size and number of lateral thecal cladia make it possible to distinguish 3 concurrent forms formally recognized as species, but the biological value of the observed differences is obscure.

THE NATURE OF THE SPECIATION EVENTS IN LINOGRAPTIDS

Some of the speciation events (transformations) observed in linograptids seem to involve the mechanism of polymorphism. Their primarily monomorphic populations became polymorphic due to the appearance of discrete morphs co-occurring within a single breeding community. This is especially apparent in the case of *Neodiversograptus nilssoni* and probably also in the *Linograptus/Abiesgraptus* transition (herein, pp. 257–258). As such morphs are kept in a population at more or less stable frequences, and the ensuing situation may be regarded as tantamount to balanced polymorphism, one of the classical microevolutionary mechanisms! In spite of considerable morphological differences between the new (mutant) morph and the primary ("wild") one, they composed a single breeding community. Although variation was represented by discrete classes, their reproduction was probably continuous.

A similar situation is described in JAANUSSON's (1981) model of a dithyrial population, which opens up alternative pathways of further evolution. The linograptids, however, tended to use only one opportunity, that of eliminating one morph and fixing the other through a shift to transient polymorphism. The immediate effect was the lack of splitting of the lineage (bifurcation). Thus the mechanism of transient polymorphism may be largely responsible for the preservation of the cohesion of the sequential linograptid species and for the prevalance of the anagenetic component over the cladogenetic one in their evolution (cf. p. 262 herein). In the case of *N. nilssoni/N. beklemishevi* transition, one could visualize the fixation of diversograptid morph in terms of geological time, as a rather rapid shift. Biologically, however, such change could occur through great number of generations. The resulting monomorphic populations, probably appeared prior to *L. progenitor* Zone, and due to it morphological features should still be assigned to *N. nilssoni*. Hence the shift in polymorphic composition of the ancestral species, had only infraspecific consequences. It was only later evolution, which involved gradual microevolutionary changes ("improvements") of diversograptid morph (Fig. 12A–C), that brought transspecific effects.

One can assume that in spite of their distinct macroevolutionary bearing, speciational events in linograptids were governed by classical microevolutionary mechanisms (balanced and transient polymorphism). At the same time, generation of variation involved sharp morphological discontinuities com-

Early evolution of linograptids explained in terms of genetic polymorphism: A, monomorphic populations of the ancestral species, composed solely of monograptid (unipolar) colonies; A', B, appearance of polimorphism due to origin of diversograptid (B) morph and its co-occurrence with monograptid (A') one. Morphologically both morphs (M) represented discrete phenotypes, but reproductively were interbreeding (R₁). This single breeding community corresponds to balanced polymorphism and may be classified as dithyrial population, as it opens alternative pathways of further evolution (symbolized by the two gates!). The later breaking down of the common breeding system occurred probably due to selection against the heterozygotes (R₂) and implies transient polymorphism. Further evolution included elimination of the monograptid morph (A') as well as the survival and subsequent improvements of diversograptid morph (B).

bined with reproductive continuity within the population. This single process acts as a lens focusing theoretical postulates of both gradualism and punctualism. Moreover, one cannot reasonably insist on the decoupling of micro- and macroevolution. There is also more evidence of the significance of polymorphism and shifts from its balanced forms to the transient ones in the evolution of graptoloids (cf. SKEVINGTON 1967 for *Nicholsonograptus*, and URBANEK 1970 for the appearance of so-called *veliger* morph in *Bo-hemograptus*, as well as RICKARDS *et al.* 1977, for the origin of an early monograptid, *Monograptus ceryx*, from its biserial glyptograptid ancestor).

The three distinct species recognized within the ancestral-descendant sequence composing the linograptid lineage as defined above (*nilssoni-beklemishevi-posthumus*) are linked by some populations having a less definite taxonomic status. By definition, they coincide with the speciation events, understood herein as periods of relative condensation of phenotypic changes. Thus an intermediate population, (sample A), occurs between *N. nilssoni* and *N. beklemishevi*. This is indicated by its position (a Baltic erratic boulder from the *parascanicus* Zone), that is distinctly above the top of the *nilssoni* Zone, but somewhat lower than the occurences of typical *N. beklemishevi*. As seen in Fig. 3A, specimens from such a population display a combination of characters typical of ancestral *N. nilssoni* (e.g. a single sicular cladium with a holoperipheral 1^2 !) as well as of the descendant species *N. beklemishevi* (a symmetric position of the dorsal apertural spine.).

In spite of the incompletness of the record (see p. 250 for the suggested explanation), the occurrence of such intermediate forms is indicative of an essentially gradual course of phenotypic changes between the typical populations of both the species in question.

Although the structure of the sicula is difficult to recognize on flattened forms, the specimens of N. *nilssoni* described by PALMER (1971) from Long Mountain, Welsh Borderland seem to show both an asymmetric dorsal apertural spine (his fig. 4) as well as a symmetric one (shown in his fig. 6). The stratigraphic position of both forms is defined as the *nilssoni* Zone, but the symmetric siculae probably developed somewhat later and might occupy the intermediate position similar to that of population A described above.

Another intermediate population, named B, was recognized in the *leintwardinensis* Zone (the Mielnik deep boring). The rhabdosomes has essentially *beklemishevi*-like siculae, but showes a linograptid divergence of the dorsal spine (D_A) of some 150°. This contrasts with the straight, forward-oriented dorsal apertural spine of the metasicula in the *N. beklemishevi* populations from the underlying *scanicus* Zones.

This structure might have preceded the restructuring of the sicula exhibited by more advanced linograptids. There were two stages in this restructuring, namely the change in the proportion of the sicular segments and a fairly radical transformation of the virgella. The former led to a certain increase in the total length of the sicula, with a greater share of the prosicula and a proportional shortening of the metasicula. Morphologically, these changes are not especially impressive. Biologicaly, however, they may be quite important (see p. 249 herein).

The transformation of the virgella into a robust rod which terminates with a virgellarium – a specialized apparatus of a largely enigmatic function – is a more spectacular event. The starting point of this transformation may be seen in deviation of the virgella in advanced populations of *N. beklemishevi* (Fig. 3C), attaining some $20-22^{\circ}$, equal to that in *L. posthumus* and twice as big as in typical *N. beklemishevi* ($10-12^{\circ}$). As traced in the fossil record available, the emergence of the virgellarium seems to be abrupt, since the Lower Přidoli colonies already display a complete apparatus (p. 240 herein). ŠTORCH (1995) has recently found typical virgellaria in *Linograptus posthumus* from the *kozlowskii* Zone (early Ludfordian) of the Barrandian area. However, there is little doubt that the sudden appearance of a "ready-made" complex structure is only an effect of the incompletness of the record, as well as the extreme fragility of the virgellarium, which happens to be preserved only very rarely.

In general, it seems fair to conclude that the differences between *N. beklemishevi* and *L. posthumus* exceed those between *N. nilssoni* and *N. beklemishevi*, and that a certain discontinuity recognized here is only to some extent bridged by intermediate population B (see diagram, Fig. 17 suggesting a change in the direction of the evolution). Ranked taxonomically, these results can be evaluated as the appearance of a new genus.

The scarcity of transient populations between *N. nilssoni* and *N. beklemishevi* as well as between the latter and *L. posthumus* can easily be ascribed to facial changes involving both the palaeoenvironmental and the presevational factors.

However, the entirety of the data are indicative of a probably non-random nature of this scarcity as other graptolite lineages flourished in the epicontinental Ludlow seas of Europe during the *nilssoni-be-klemishevi* interval. It seems that temporarily the numerical abundance of the linograptids must have been drastically reduced as they were simply outcompeted by cucullograptids at least in the shelf biota. This does not exclude, however, their greater abundance in the neritic and pelagic realms. Great biotic changes in the *leintwardinensis* Zone (URBANEK 1970) triggered not only the exctinction of cucullograptids, but also, with a certain delay, the reappearance of the linograptids in the shelf waters; it opened new prospects for other survivors as well, namely neocucullograptids. A great abundance of *L. posthumus* after the extinction of the last named group during the *Neocucullograptus kozlowskii* Event, observed in the Mielnik bore core, may also be interpreted as evidence of a competitive replacement.

A close relationship between *Linograptus posthumus* and *Abiesgraptus tenuiramosus* is indicated by the linograptid stage in the astogeny of the latter species. However, from its first appearance, *Abiesgraptus* has all its characteristic features fully developed. They include: a tetrameric (four-branched) foundation of the rhabdosome; an ability to generate, on the main branches of the rhabdosome, paired lateral thecal cladia with a regular spacing between them; and a secondary flattening of the central (sicular) portion of the rhabdosome,

i.e. the spreading of the four main cladia in one plane and the obliteration of the divergence angle between the branches at the proximal end, which was characteristic of *Linograptus*. The two first features emerged gradually in the zonal evolution of the *Linograptus* populations. Thus, the four-branched rhabdosome became the predominanting form of the colony within the Lochkovian populations of *L. posthumus*, producing in this way a necessary prerequisite for the origin of *Abiesgraptus* (p. 241).

As was directly observed in the *Linograptus posthumus* specimens from the *uniformis* Zone (JAEGER 1969), the proximal part of the giant tetraramous rhabdosomes produced regular quadrants with the angles between the armpits being nearly orthogonal (measured angles are $80-100^{\circ}$ and frequently 90°). These large-sized colonies were "floating crosses", with distal parts of their cladia bending freely due to their natural flexibility. In the vicinity of the sicula, the distances between the zooids situated on the adjacent cladia were small and consequently their depletion zones were overlapping. This probably resulted in a severe competition among the proximally placed zooids. The situation was improving in the course of the growth and expansion of the colony, due to increasing distances between more distally placed zooids. As the growth progressed, the terminal zooids situated on the tips of the expanding colony were in a favourable position, having no competition. However, the total harvesting efficiency of the colony was deteriorating, due to a fairly rapid increase of the area available as compared with the moderate increase of the number of zooids present. More and more area remained underutilized and the terminal zooids more and more "lonely" (a similar conclusion was reached by JAEGER 1969: pp. 493–494). The rotation of the rhabdosome.could only partly improve the harvesting efficiency and large-sized tetraramous colonies remained rather inefficient. In terms of the utilization of the resources available, such colonies were probably less effective than their Ludfordian-Přidoli forerunners, with several cladia radiating from the sicula and penetrating more or less uniformly the surrounding space. A radical improvement did not come until the lateral cladia were invented. Situated on the main cladia and oriented normally to them (Fig. 6, L), they penetrated the free space available within the armpits of tetrameric colonies. Such pattern ensured a better use of the resources around the colony (see also JAEGER 1969: p. 494). Therefore, the appearance of the lateral cladia, even sporadic and irregular, presented a distinct adaptive advantage over the tetraramous rhabdosome and was favoured by selection. Hence, I see the origin of Abiesgraptus (discussed at some details below) as a process controlled by a strong selection pressure.

From the above considerations one can deduce that the increase of the number of zooids in each cladium should follow the formula: N = k l, where k is a specific coefficient showing the increase of the number of thecae per 1mm (for L. posthumus its value is about 0.7), and l is the distance from the sicula (in mm). Hence, the total number of thecae in a tetraramous colony is 4N. On the other hand the area (a) exploited by a given colony at a certain growth stage is equal to the surface of a circle with a radius l, namely $a = \pi l^2$. The harvesting potential of the colony may be estimated using the relation 4N/a. Some parameters for a growing L. posthumus colony are shown on Fig. 13A, B.

One more measure is the degree of "loneliness" of the terminal zooids situated on the growing tips of the colony, namely the calculation of the distance of each zooid from its terminally situated neighbour on an adjacent cladium. With a certain simplification (small differences in the length of cladia being neglected), this distance (d) may be calculated from the formula, $d = \sqrt{2l^2}$. From this it follows that contrasts which develop in a growing *Linograptus* colony are caused by the arithmetic progression of the number of zooids N, and the geometric progression of the area exploited, a.

The ability to form lateral thecal cladia appeared early in the phylogeny of the linograptid lineage. This may be indicated by the sporadic occurencies of such cladia, either paired (TELLER 1964, on a three-branched rhabdosome from the early Přidoli) or single asymmetric (JAEGER 1969, from the early Lochkovian on a four-branched rhabdosome). The irregular generation of thecal cladia in *L. posthumus* could be interpreted as an imperfection of the morphogenetic control of this evolutionary novelty, which later was subject to a rigid pattern formation. The horizontal disposition of the three cladia radiating from the sicula probably means the reestablishment of the *N. beklemishevi* condition of growth and *per se* is rather a minor change. Combined, however, these three features brought about the origin of *Abiesgraptus*.

The *Linograptus/Abiesgraptus* transition was in fact rather unconventional, namely it was a transformation in large sympatric populations. Both parameters – the sympatry and the large size of populations involved are in strong opposition to the recent orthodoxy in the field of the origin of species (MAYR 1982). In the latter parameter (large population size), the appearance of *Abiesgraptus* also differs from two other instances of species transformation in the linograptid lineage, suggesting a certain reduction of the

Fig. 13

Stages in the development of cladia (A) and main parameters (B) in a growing tetraramous *Linograptus* colony. Rapid expansion of the colony due to budding of new zooids on the growing tips of four cladia led to an increase of their total number (4N) and to elongation of each cladium (l, in mm). Increase of distances (d) between zooids reduces the competition between individual zooids, thus improving their feeding conditions. At the same time the geometric progression of the area (a) of the potential exploitation (shown for the convenience in cm^2) and the relation 4N/a (shown for the convenience \times 10) are indicative of an increasing underutilization of the resources potentially available as the colony expands. For further explanations see text.

population size at least in the epicontinental seas and the bottlenecking of the lineage (see p. 250). A fairly rapid morphological evolution as observed in the *Linograptus/Abiesgraptus* transition, suggests that graptolites, possibly hermaphroditic clonal organisms, were capable of using some "non-conventional" mechanisms, e.g. self-fertilization followed by instant homozygotization (cf. URBANEK 1990). Although purely hypothetical, such mechanisms shed some light on this otherwise paradoxical pattern of species transformation.

The record available does not permit a safe recognition of the mode of speciation in *A. tenuiramosus*. JAEGER (1959) was convinced that in the *praehercynicus* time *Linograptus posthumus* and *Abiesgraptus tenuiramosus* had been two morphological forms of the same breeding community, and at that time they could have been assigned to a single species. This still leaves room for different interpretations. Were these forms two morphs (namely, the *linograptid* morph which was not capable of attaining the abiesgraptid growth stage and the *abiesgraptid* morph proper which passed through an earlier linograptid

Conceptual diagram showing the main events in the emergence of *Abiesgraptus* pattern of colony organization. Two independent directions of changes leading to B_1 and B_2 may be derived from ancestral type of *Linograptus*, represented by A. The crucial event is represented by C, where disparate features, acquired within these two lines, were combined into an adaptive syndrome, later improved and transformed into the perfect, compound colony of *Abiesgraptus* (**D**). Further explanations in text.

growth stage), coexisting within a single population (polymorphism) or was every colony potentially capable of attaining the abiesgraptid characters at some stage of the astogeny? In the first case, the later speciation resulted most probably from transient polymorphism with the elimination of the less advanced morph. The second possibility implies a gradual increase in frequency, expressivity and penetrance of genetic factors responsible for the formation of lateral cladia in tetraramous rhabdosomes, hence, a shift of the mean towards a greater frequency of lateral branches, which started to appear at earlier stages of astogeny (acceleration).

But was the story as simple as that? I would argue for a different scenario of the *Linograptus/Abies-graptus* transition in view of a gradual and heterochronic appearance of disparate abiesgraptid features within the early linograptid populations. On one hand, some large-sized and four-branched *Linograptus* colonies from the *uniformis* Zone are still deprived of thecal cladia (JAEGER 1969), on the other, lateral branches may occur as early as the lower Přidoli and be situated on three-branched colonies (TELLER 1964). It is clear, therefore, that the potential for generation of lateral cladia appeared early in the phylogeny and obviously was not correlated with the simultaneous formation of tetraramous conditions. The interpretation which, in my opinion best fits the record seems that which claims that the morphotypes shown on Fig. 14 B₁ and B₂, and tentatively named pseudo-*Abiesgraptus* and para-*Abiesgraptus*, evolved within two different semispecies. Each of them showed a distinct trend in variation, directed towards the formation of either a tetrameric foundation of the rhabdosome (*tetra*) or lateral branches (*lat*). This may explain the disparate origin of both features, which was followed by a secondary integration of the species genetic system by means of hybrydization or introgression (Fig. 14C). As a result the two

Fig. 15

Ideogram showing the significance of presumed patchiness in linograptid distribution for the disparate origin of evolutionary novelties. Upper part of the figure: the occasional gene flow due to migration (black arrows, 5) between individual patches **A**, **B**, **C**, with different genetic structure (1–3), ensures the appearance of a compound genotype in **C**, which subsequently may spread (white arrows, 4) due to its high fitness. Lower part of the figure: a similar effect due to the merging of the patches **A**₁ and **A**₂, followed by an introgression (**C**₁) and the appearance of a compound genotype. Fit genotype may later spread rapidly (white arrows, 4).

independently acquired unit characters *tetra* and *lat*, became components of a single synthetic morphotype, represented by proto-*Abiesgraptus (tetra-lat* morphotype). The above considerations may be tabulated as follows:

morphotypes/ populations	tetra	lat
B1	-	+
B ₂	+	122
С	+	+

Note: B₁, B₂ and C refer to Fig. 14.

The resulting compound rhabdosome displayed an irregular branching pattern (inherited from pseudo-*Abiesgraptus*), later subject to selection pressure and an increased morphogenetic control (Fig. 14D). The attaining of the abiesgraptus stage in the morphological organization of the colony is clearly a transspecific event. As correctly emphasized by JAEGER (1959), the origin of *Abiesgraptus* means the beginning of a new direction of evolution with a new evolutionary prospect – the emergence of a new genus seen *in statu nascendi*.

It seems almost certain, that in the area of their distribution, planktic linograptids formed a system of semi-isolated populations (patches). Patchiness is a remarkable feature of plankton biology recognized by modern studies (BOXSHALL 1981; BARRY and DAYTON 1991) and used in order to explain a number of phenomena (such as sympatry of a great number of rather similar taxa or the "paradox of plankton" as defined by HUTCHINSON 1959, 1961). Each individual patch is in fact a huge deme of a certain duration in time, the longevity of a given patch being largely proportional to its size. Linograptids as the dominating group of Late Silurian macrozooplankton were surely subdivided into numerous and relatively large patches. Such spatial organization is considered by some authors (e.g., GRANT 1977) to be most favourable

Fig. 16

Possible genetic mechanisms involved in the emergence of an adaptive syndrome. I – patches A, B, C comprising disparate unit characters merge into a common megapopulation (II – ABC) enabling further recombination due to crossing. III–V successive changes in the genetic structure of population from initial frequencies (p_0) of genes responsible for corresponding unit characters (III), through their combinations (only some shown) displaying frequencies p_1-p_4 controled by selection, until superior genotype ABC appears (IV), and is fixed as an adaptive syndrome.

for macroevolutionary changes. Some of recent models advanced to explain genetic polymorphism in krill populations assume that pelagic plankton species are partitioned into numerous patches and that selection is sensitive to differences between the patches (AYALA and VALENTINE 1979; BUCKLIN 1986). I will proceed from a similar assumption.

Each patch probably behaved as a partly autonomous unit ("a floating island") where variation, either generated *in situ* or introduced by an occasional gene flow between the patches, accounted for more or less unique genotypic combinations (Fig. 15A, B, A_1 , A_2). One could believe that patchiness was involved in producing the disparate *Abiesgraptus* features and then bringing them together into a characteristic compound or an adaptive syndrome (Fig. 15C, C_1). The patchiness was probably responsible for the origin and maintenance of distinct trends in variation, interpreted above as semispecies. Some events were taking place in semi-isolated systems, producing distinct morphotypes. The cohesion of species' genetic system was, nevertheless, preserved as the evolving populations eventually reunite due to hybridization or introgression, before attaining the reproductive isolation.

The disparate origin of the adaptive characters may be due to a heterochronous and independent appearance of the component parts ("unit characters" as *tetra* and *lat*, see above). Each of them was advantageous under certain circumstances, but when combined into a syndrome (a coordinated complex structure, as *tetra-lat*), they produced the highest fitness, probably as a result of a synergetic effect. In the instance represented by the *Linograptus/Abiesgraptus* transition, particular elements of the future adaptive syndrome must have appeared successively in local populations (patches) to be later assembled by means

of a sexual process into a syndrome (Fig. 16, I–II). The genetic and selective mechanisms that were most likely involved in the syndrome formation are shown in Fig. 16, III–V. It is assumed that simple combinations (AB, BC, AC) had a selective advantage over single characters (A, B, C) and, in turn, the compound genotype (ABC) was superior to all the remaining combinations. Such a piecemeal pattern of the emergence of a complex adaptive structure seems not only more probable than its instant origin, but is, at least partly, supported by the fossil record. Another remarkable feature of the *Linograptus/Abiesgraptus* phyletic transition is world-wide distribution (probably warm-water cosmopolitism) of both ancestral and descendant species. This may imply a polycentric or even pantopic appearance of the new species, over large areas within the range of the parental taxon, instead of its local, sympatric or allopatric origin as usually presumed. It seems unlikely that such a wide geographical distribution could have been attained due to migration within so limited a time.

The above disparate mode of the appearance of new characters in the linograptids is only a special case of the mosaic course of evolution. This classic palaeontological rule (also known as the Watson Rule) has recently been elevated by STEBBINS (1983) to the rank of "an integrating principle for the modern synthesis".

EVIDENCE FOR PHYLETIC EVOLUTION IN THE LINOGRAPTID LINEAGE

The evidence available indicates that throughout almost all its history the linograptid lineage was represented, at any given time-level, by a single morphospecies. This is certainly true for the sequence: *Neodiversograptus nilssoni–N. beklemishevi–Linograptus posthumus*. The subspecies of the latter, namely *L. posthumuus tenuis* (JAEGER, 1959), is in every respect identical with the type species, except for smaller size, and may rather represent a zonal variety. Less certain is the nature of *Linograptus phillipsi* described by DECKER (1935, 1939) from North America. Its remains need a modern revision, but for the time being it can be treated as a geographical variety of the European species, whilst var. *multiramosus* is simply an astogenetic variant. Numerous subspecies or species of *Linograptus* erected by Hundt are all of preservational or astogenetic nature (see JAEGER 1959: pp. 143–144).

The Linograptus/Abiesgraptus' transition as well as the later Abiesgraptus diversity need, however, additional comments. The overlap in the vertical range of L. posthumus and A. tenuiramosus as observed by JAEGER (1959) in the praehercynicus Zone may be more apparent than real, since juvenile rhabdosomes of Abiesgraptus cannot be distinguished from the Linograptus colonies. This occurs because, in its astogeny, Abiesgraptus possesses the Linograptus growth stage (compare p. 241 herein) which can be identified taxonomically as Linograptus. Thus, this overlap is most probably illusory and does not mean a real co-occurrence of the two species in question. As mentioned above, it is more probable that A. tenuiramosus originated from L. posthumus by means of sympatric transformation and replaced it as a new chronospecies, after its disparate characters were united into a syndrome.

The next case to be explained in the context of the phyletic nature of the evolutionary changes in linograptids is the "terminal variation" of Abiesgraptus expressed in relatively small differences in the width and the size of the branches. This variation was used to discriminate formally valid species, such as A. multiramosus and A. longiramosus, both accompanying the standard form of A. tenuiramosus. This may imply multiplication of species and branching of the lineage. However, even if these differences were sufficient to distinguish separate species (which is not perfectly clear), the diversification, immediately preceding the extinction of the lineage, occurred too late to change the general sequential nature of the speciation events within linograptids (diagram Fig. 17). Another instance of increased morphological diversification in phylogenetically late stages of Abiesgraptus lineage was described by LENZ (1988). His fragmentary specimens from fanicus Zone (Pragian) of northern Yukon (Canada), exhibit first and second order cladia, arising in pairs or singly from the primary stipe. Such features were never seen in earlier representatives of the genus and the Yukon species marks the latest occurrence of the lineage. Most likely it produced a short offshoot of the abiesgraptid stock, being the last attempt at a progressive development of the compound rhabdosome. This attempt failed after a short success in a probably restricted area. Hence, the latest representatives of Linograptinae display an increased amount of variation and a tendency towards splitting of the lineage just before its final exinction. These phenomena may be best explained assuming

SIMPSON's (1944) idea that extinction in many cases is preceded by an increased splitting of the endangered groups or lineages, trying to find out an adequate adaptive response to the changes of the environment.

The application of the morphological species concept to the evolution of lineages is in general charged with danger of treating morphotypes as separate species. Thus common co-existence of two morphotypes, A and B, might be interpreted as their co-occurrence, whilst in fact they represent a polymorphic population (a polymorphic chronodeme) rather than anything else. The same holds for the growth stages in compound colonies, as is the case with the unipolar and bipolar stages of *Neodiversograptus nilssoni* (or *Linograptus/Abiesgraptus* as discussed above) where astogenetic variants may be ranked systematically and treated as apparent instances of co-occurrence.

As demonstrated by linograptids, a long-lasting phyletic evolution in a single lineage implies an unusual cohesion of the genetic (and epigenetic) system of the species. In spite of their world-wide distribution, *Linograptus posthumus* and *Abiesgraptus* spp. preserve a remarkably uniform morphology over vast areas. They exhibit the phenomenon of warm-water cosmopolitism, a common feature of recent plankton. The genetic and phenetic cohesion allowing such species, both extant and fossil, to avoid the consequences of isolation by distance, presents one of the unresolved "paradoxes of plankton".

The evaluation of the entire picture of the linograptid evolution is an uneasy task. Following the reasoning presented by HALLAM (1982) for Jurassic *Gryphaea*, the periods with an increased rate of morphological changes observed in the phylogeny of the linograptid monophyletic lineage may formally be interpreted as punctualism. This is, however, an extrapolation of the primary meaning of the notion directly related to the multiplication of species and branching of a lineage (ELDREDGE and GOULD 1972).

Neither the Gryphaea nor the Linograptinae provide convincing evidence for branching events (bifurcation) and consequently there is no stratigraphic overlap between the ancestral and the descendant species. Members of the lineage are in both cases sequential species (chronospecies), displaying, however, an increased rate of morphological changes during the periods coinciding with transformation (phyletic speciation). The term *punctualism* can safely be applied to describe the changes observed in the lineage of Metrarabdotos, a Neogene bryozoan, where each speciation is associated with the branching of the lineage and the co-occurrence of the parental and the daughter species (CHEETHAM 1987). In linograptids, the morphological changes are not so strongly punctuated (in Metrarabdotos, morphological changes within the confines of the species are practically equal to zero, and the entire morphological change is due to speciation; in the Gryphaea, the situation is largely similar), and the stasis does not mean an almost complete arrest of change. Taking into account the sequential nature of the linograptid species and the above-mentioned characteristic of the speciational events in their lineage, one could perhaps define this mode of evolution as quasi-punctuated. A number of technical terms were suggested to describe this situation, which only partly correponds to the punctuated model of speciation (condensation of morphological change in time but no splitting and prevalence of anagenesis), to mention only punctuated gradualism (FENSTER et al. 1989) or punctuated stasis (SPRINGER and MURPHY 1994).

LINOGRAPTID PHYLOGENY AS AN INSTANCE OF MACROEVOLUTION

As compared with a number of classical examples of macroevolution, frequently quoted in the neontological (e.g. Darwin's finches of the Galapagos Islands and the Hawaiian honey creepers) and current palaeontological literature (ELDREDGE 1989), linograptids possess some unique features. First of all they represent a single lineage, almost devoid of any offshoots, that is an unbroken chain of the ancestral-descendant succession of populations. The pattern of linograptid evolution is therefore characterized by a strong anagenetic component and a very weak cladogenetic component (as defined by HUXLEY 1958 and applied to graptolites by BULMAN 1963).

The predominance of anagenesis in the linograptid evolution is most probably the result of long-lasting directional selection leading to the stepwise improvements of the adaptive type through distinct structural changes of the colony organization. The absence of a pronounced tendency toward multiplication of the species speaks for a great cohesion of the population genetic pool at any particular time, most probably due to a strong action of stabilizing selection associated with the directional vector of selective forces. Stabilizing selection counteracted any disruptive effects or splitting the genetic system of the species. As

a result, the linograptid evolutionary changes were strongly canalized, and the main "trials" concentrated along the pathways leading towards multiramous compound colonies.

Within this single line of descent the Linograptinae realized large-scale evolutionary changes, producing new patterns of colony organization and at least three distinct adaptive types. In consequence, the entire evolutionary potential of evolving populations was profoundly changed. The appearance of new transspecific taxa (3 genera, 1 subfamily), new structural types, and great adaptive (ecogenetic) consequences are prima facies characteristics of macroevolution. Ample speciation may logically be considered only a side-effect of macroevolution, but not a primary feature of the process. Such commonly cited examples of macroevolution as the Hawaian honey creepers or the Galapagos finches display a distinct prevalence of speciation over morphological changes, with the key structural type remaining little affected by evolutionary change. They are more representative as illustrations of adaptive radiation than as exponents of macroevolution. Such instances were used for punctualistic generalizations concerning the predominance of the speciational component in macroevolution over the phyletic one. The history of the Linograptinae offers a different logic and corroborates the opposite view (see Fig. 17).

The case of the Linograptinae undermines the common belief based on a punctualistic approach that an increase in the rate of morphological changes, following a period of stasis, necessarily or almost universally means branching of the lineage (splitting or multiplication). It may equally represent an accelerated phyletic transformation, that is sequential replacement of one chronospecies by the other (cf. p. 253). The stasis as observed in linograptids means a slowdown of the morphological rate of evolution, rather than a complete arrest of change. During the stasis the microevolutionary mechanisms might accumulate variation of great significance for the prospective evolution. The phenotypic expression of these newly appeared variants exhibits a low degree of morphogenetic control which is manifested by the changing localization of the gene action and an imperfect symmetry of the phenodeviants (cf. p. 256 herein).

Fig. 17

Diagram showing the main features of evolution in Linograptinae. Note the posible bottleneckings of the lineage, the position of transitional populations A and B, as well as the transformation in large populations and the terminal splitting of the lineage, before the final extinction. Further explanations in text.

Theoretical models of macroevolution are usually based on generalizations of large bodies of empirical data combined with some deductions from the accepted theories in different fields of biological sciences. A single case can hardly be used in their falsification since they could only be tested against a larger class of empirical data. Nevertheless, it is always important to see to what extent the parameters of the phenomena observed fall within the range of values or predictions compatible with the current hypotheses or models.

In this review I will consider only some conclusions which can be drawn from the linograptid case against a wider theoretical background.

The evolution of linograptids offers no evidence in support of saltationary concepts of macroevolution. There are no data indicative of a sudden appearance of new structural types which could have been ascribed to large mutational events. Though the generation of a new cladium does produce an abrupt phenotypic effect, the discontinuity here is secondary, due to a meristic nature of the character involved (an increase in the number of morphological units, a sort of polymerization). However, it is clear that the new patterns were fixed in a stepwise manner, the entire picture suggesting an additive piecemeal "technology" rather than great evolutionary leaps. The presence of well-defined, but intergrading chronospecies, whose phenotypical traits are gradually modified, may be better explained within a neo-Darwinian paradigm.

The pattern of the linograptid evolution only partly corresponds to the punctuational model. Thus phenomenologically, the stasis observed in the linograptid species equals that distinguished by punctualism, but it should probably be ascribed to a certain mode of action of natural selection. There is no substantiation for the essential decoupling of micro- and macroevolution, and frequently the microevolutionary changes have a great bearing on the phylogenetic future of the species (see also URBANEK 1970). The bottlenecking without the splitting of the lineage, as observed in the nilssoni/beklemishevi and beklemishevi/posthumus transitions, does not fully correspond to the model of rapid speciation as suggested by the concept in question. Such events as gradual transformation in large populations (L. posthu*mus*/*A. tenuiramosus*) or major morphological transitions within a single lineage should be considered by punctualism as practically impossible or quite exceptional. It is also very difficult to make inferences about the causes of past processes from the information available presently on speciation. Opinion is still strongly divided into the adherents of founder-induced speciation, which ascribe great role to the bottlenecking as a precondition for genetic revolution (CARSON and TEMPLETON 1984), and the followers of a quite opposite view that speciation may proceed in moderate or even large size populations by gradual divergence of gene pools (BARTON and CHARLESWORTH 1984). The linograptid case offers some support for the view that both modes of speciation may be involved in the evolution of a single lineage (Fig. 17).

The abiesgraptid growth pattern of the colony seems to be adaptively superior to that represented by the majority of Lower Ordovician multiramous colonies (the Anisograptidae and Dichograptidae). Branching in the last named groups was based on planar bifurcation at a certain angle, and the continuing growth of the rhabdosome (elongation and dichotomy) was constrained by the mutual impinging of the stipes. Such conditions imposed important limitations on the branch configuration in the Ordovician multiramous groups. Abiesgraptids solve this problem in a more satisfactory way, because their lateral branches, although planar, are parallel and situated on the two opposite main branches, thus excluding any impinging (Fig. 6). It is obvious that the appearance of this improved pattern was preceded by less fit "trials", some of which were eliminated by natural selection.

Acknowledgements. — I express my gratitude to the participants of the Group on Organismic Evolution on the Dahlem Workshop "Patterns and Processes in the History of Life" (June 1985), where I first presented some of my preliminary conclusions concerning the evolution of linograptids. The exchange of opinions was truly stimulating. This paper benefited from the discussion I had with Hermann JAEGER, a few month before his death. I thank Anna KOZŁOWSKA-DAWIDZIUK who provided data from her unpublished MSc dissertation. Thanks are also due to Mrs Irina BAGAJEWA-URBANEK for translating this paper into English. The final phase of the research was supported by the Grant No 600 36 91 01 from the Polish Committee on Scientific Research.

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THE EMERGENCE AND EVOLUTION OF LINOGRAPTIDS

PLATE 1

1-5. Early stages of cladial generation (1a, 2, 3), details of virgellarium (1b) and thecal characters (4, 5) in *Linograptus posthumus* (Reinhard RICHTER, 1875); 1a sicula with theca 1¹ of the procladium and theca 1² of the first sicular cladium. Note the presence of virgellarium (Vg) preserved in its relation to the sicula and shown in an additional aspect (1b); 2, 3 slightly deformed apertures of metasicula (Si) with sicular cladia radiating from it; 4, 5 apertural parts of distal thecae with genicular ventral wall and apertural lip somewhat introverted. Mielnik-1 borehole; 1 depth 792.25 m, early Ludfordian, *acer* Zone, × 75; 2, 3 depth 764.15 m, late Ludfordian, *protospineus* Zone, 2 × 100; 3 × 175; 4, 5 depth 873.60 m, early Ludfordian *inexspectatus-kozlowskii* Interzone. Si – sicula, Vg – virgellarium, 1¹–1³ – first thecae of respective cladia.

