The phylogenetic debate on the affinities of graptolites. An attempt at a methodological analysis

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The debate on the graptolite affinities provides a model of lasting phylogenetic controversy which may be analysed in terms of philosophy of science. As suggested by Popper, all scientific discussions start with a problem formulated within the context of a certain problem situation which develops as a result of the growth of knowledge. About 10 such problem situations may be distinguished in the debate analysed, beginning with the multiparadigmatic stage in the late 19th century. At this time the coelenterate paradigm was elevated to the rank of canonical knowledge of the time. The 1930s saw the culmination of the debate with the revival of classical concepts of graptolite affinities – the coelenterate and the bryozoan paradigms. The most important event was, however, Kozłowski's radical modification of the pterobranch paradigm. The present views on the graptolite ancestry may be directly derived from Kozłowski's great contribution. New palaeontological evidence supplied by Kozłowski, and the palaebiochemical studies by Foucart et al. in 1960s outweighed the alternative viewpoints and Kozłowski's concepts were generally accepted.

The TEM studies by Urbanek and Towe detected, however, an esssential dissimilarity in the ultrastructure of the graptolite and the pterobranch periderms. This anomaly was difficult to explain within the framework of Kozłowski's concepts and led to Urbanek's temporary revival of views declaring the graptolite ancestry an open problem. Anders and Crowther and Rickards discovery of cortical bandages provided new evidence for uniform mode of secretion of the pterobranchs and the graptolite skeleton. Recent biochemical data indicating a collagenous nature of the skeleton in pterobranchs in conjunction with the results of the TEM studies on the collagen-like nature of the graptolite skeleton speaks in favour of a close phylogenetic relationship between the groups in question.

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Introduction

The problem of graptolite affinities provides a classical example of a lasting phylogenetic debate which deserves to be analysed in terms of the philosophy of science. There is no doubt that such an analysis may offer an interesting lesson for palaeontologists as well as for biologists or philosophers. Also the most recent views cannot be considered in isolation from earlier concepts. The current ideas on the graptolite affinities become more understandable when their genealogy is exposed.

According to Popper (1979), all scientific discussions start with selecting a problem (P) to which a tentative solution or a tentative theory (TT) is offered to be later subject to criticism and revision in an attempt at error elimination (EE):

$$P_1 \rightarrow TT_1 \rightarrow EE_1 \rightarrow P_2 \rightarrow TT_2 \rightarrow EE_2 \rightarrow P_3 \ldots$$

Problems (P) are always formulated within the context of a certain problem situation (PS) that develops due to the growth of knowledge. The problem situation exerts a kind of pressure on the way of thinking of a scientists: PS $\rightarrow$ P. This relation implies a loose dependence rather than rigid determinism.

Primary ideas

Mutatis mutandis, the Popperian scheme may be used when trying to make sense of the extended phylogenetic debate on the ancestry and the systematic position of graptolites.

The essential problem of this debate was formulated early and has remained basically the same troughout the discussion: What are the nearest relatives (if any!) of graptolites or, in other words, what is the systematic position of graptolites in the animal kingdom?

The formulation of the problem (P) has not been, however, entirely invariant depending largely on the changing elements of the developing problem situation (PS) – thus it has a changing context.

A new problem situation emerged in each case as a result of the growth of knowledge either in the sphere of theoretical generalizations with the ensuing changes in the methodological approach or due to the influx of new data concerning the graptolites and their potential relatives.

The pre-Darwinian period had its own logic and was predominated by the problem of the nature of the graptolite remains:

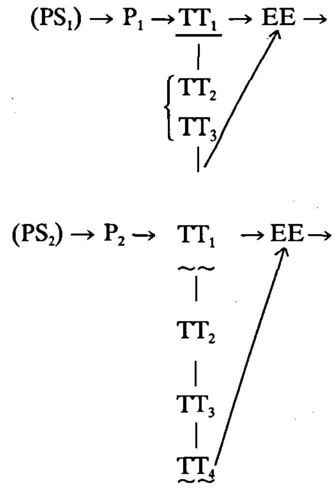
- were they inorganic or organic? – Carl Linné in "Systema Naturae", 1735;
- were they remains of marine plants? – von Brommel (1727), Brongniart (1828);
- were they fossil cephalopods? – Walch (1771);
- did they have a "polypide" or a generally coelenterate nature? – an idea which appeared around 1830 and is ascribed to Nilsson. Of all possible solution the latter idea proved to be the most fertile and was supported later by many distinguished palaeontologists.

In the post-Darwinian period of the 19th century, the logic of considerations was radically changed owing to the spreading of evolutionary thinking and introduction of phylogenetic notions.

This led to the emergence of a new problem situation (PS_1), and the primary pool of ideas was formulated. About ten (10) problem situations (PS_1–PS_{10}) can be tentatively distinguished in the course of the post-Darwinian part of debate on the graptolite affinities, each being the result of an influx of new data involving a certain way of thinking and implying a specific solution of the general problem (P). The old semi-intuitive concepts were partially tested and most of the false views were refuted.

Three main concepts (TT_1–TT_3) evolved as a result:

1) the coelenterate (and in most cases the hydrozoan) concept (Hall, 1865; Lapworth, 1873; Allman, 1872; Nicholson, 1872),
2) the bryozoan concept (Salter, 1866),
3) the *Rhabdopleura* or primaeval pterobranch concept (Richter, 1871).



a multiparadigmatic stage
—— included into the canonical knowledge (K. Zittel, "Handbuch...". 1880)
~~ the main conflicting tentative theories

Fig. 1. The anatomy of the primary pool of ideas.

The second half of the 19th century was multiparadigmatic with predominance of the coelenterate concept, which was elevated to the status of canonical knowledge in the treatise by K. Zittel (1880) (see diagram below).

C. Wiman's contribution (1895) accounted for a new problem situation (PS_2). He initiated a revolution in the techniques of graptolite research bringing about a vast increas in the knowledge of the group (see diagram above). C. Wiman (1895) advanced an agnostic theory (TT_4) that graptolites were unique and had no close affinities with other groups. His views were shared by a number of distinguished palaeotologists such as Perner (1894), Ruedemann (1895), Frech (1897) and Elles (1922).

It was Schepotieff (1905, 1907) who created another problem situation (PS_3). He proposed a redifinition of the previous ideas on the pterobranch ancestry to form the pterobranch paradigm ($TT_3 \rightarrow TT_3''$).

It should be noted that Schepotieff's ideas were an odd blend of apt conclusions and their inadequate substantiations. Thus, his conclusions concerning graptolite affinity later proved to be correct, but his homologies were entirely misleading. He believed in the existence of two homologies: between the sicula and the terminal portion of the creeping tube in *Rhabdopleura* and between the stolon of *Rhabdopleura* and the nema or the virgula in Graptoloids. Moreover, in his considerations Schepotieff underestimated the significance of the peculiar fine structure in both groups, exemplified by the presence of characteristic growth bands.

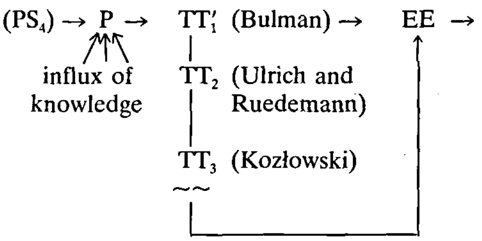
The great clash of ideas

The thirties of the 20th century saw a renewed multiparadigmatic stage associated with the redefinition and modernization of the three main paradigms: the coelenterate paradigm (Bulman, 1932, 1937, 1938), the bryozoan paradigm (Ulrich and Ruedemann, 1931), and a completely new version of the pterobranch paradigm (Kozłowski, 1938) – PS_4).

A great clash of ideas ensued and resulted in the predominance of Kozłowski's pterobranch paradigm (see diagram below). Kozłowski's classical hypothesis was based on new factual grounds: on the histology of the skeleton, and the recognition of its fusellar and cortical components; the specificity of the fusellar structure; and on the composition of the skeleton with its alleged chitinous nature. Moreover, he emphasized the significance of the presence of an internal stolon, as well as the peculiar mode of budding in graptolites.

Kozłowski's views can be summarized in three main conclusions or theses:

a) the morphogenetic thesis, stating the mode of formation of the cortex was unique in graptolites and implies the presence of an extrathecal membrane;



~~ predominating TT as a result of EE.

Fig. 2. The renewed multiparadigmatic stage (1930s).

b) the phylogenetic thesis, indicating the close affinity between the rhabdopleurid pterobranch and the Graptolithina, and

c) the new concept of the biological organization of the graptolite colonies involved, first and foremost, new interpretation of thecal polymorphism understood as an extreme case of *sexual dimorphism. Hence a great difference* between the graptolites and the coelenterates whose polymorphism is based on the division of non-sexual functions.

The recognition machinery and the discovery of an anomaly

The reception of Kozłowski's ideas was delayed because of the outbreak of World War II, but O. M. B. Bulman, the leading authority on graptolites, soon became convinced as to their pterobranch affinity. Bulman restated Kozłowski's main views and corroborated them by his own observations on dendroid graptolites (1942, 1945). Later, Bulman (1949) reported on graptolites, in connection with Kozłowski's discoveries, to the 13th International Congress of Zoology (Paris, 1948).

A great part was also played by the authors of big treatises, especially by Dawydorff (1948) in the "Traité de Zoologie", by Waterlot (1953) in the "Traité de Palaeontologie", by Bulman (1955) in the "Treatise of Invertebrate Palaeontology", and by Beklemishev in his "Principles of Comparative Anatomy of Invertebrates" (1970, 1952, 1964).

Whilst Kozłowski's ideas on the affinities of graptolites were rather widely accepted, there were some doubts concerning his concept of skeletal secretion (compare Bulman 1955, 1970). As a matter of fact, Kozłowski never defined precisely enough the topographical relation between the soft parts and the skeleton. The combination of the pterobranch and the bryozoan mode of secretion proposed by him appeared implausible to some zoologists.

Beklemishev (1951) concluded that the secretion of the graptolite periderm followed entirely the pterobranch mode. By rejecting Kozłowski's morphogenetic concepts but accepting his phylogenetic conclusions he anticipated the most recent developments.

Successive problem situations (PSS) emerging in the debate on graptolite affinities*.

* (Pre-evolutionary, incipient ideas on the nature and systematic position of graptolites are ommitted.)

Successive problem situations	Main events	Resulting theoretical situation
PS_1	Primary pool of ideas 1860–1895	multiparadigmatic stage, dominance of the coelenterate paradigm
PS_2	Contribution of Wiman 1895	formulation of the agnostic paradigm
PS_3	Contribution of Schepotieff 1905	redefinition of the pterobranch paradigm
PS_4	Redefinition of the coelenterate paradigm (Bulman, 1932, 1938) and the bryozoan paradigm (Ulrich & Ruedemann, 1931); a new version of the pterobranch paradigm offered by Kozłowski (1938)	renewed multiparadigmatic stage
PS_5	Kozłowski's big monograph (1949) and a series of his discoveries of fossil pterobranchs; Bulman's recognition of Kozłowski's concept (1942, 1955)	predominance of the pterobranch paradigm in Kozłowski's version including morphogenetic theses
PS_6	Criticism against Kozłowski's concept especially the chitin-protein controversy (Hyman, 1959).	a certain rebirth the coelenterate paradigm treated as an alternative to the pterobranch one, hesitant position in the palaeontological community
PS_7	Studies of Foucart et al. (1964, 1965, 1966) on palaeoproteins in graptolite skeleton and proteinaceous nature of pterobranch skeleton. Kozłowski's defense of his theses. (1966).	strenghening of the pterobranch paradigm completed by the biochemical data
PS_8	Discovery of an "ultrastructural anomaly", in an attempt to confirm Kozłowski's concept with TEM studies (Towe and Urbanek 1972, Urbanek & Tove 1974, 1975, Urbanek 1976) and a question raised against the validity of Foucart's results in respect of graptolites. Incongruences in Kozłowski's model of secretion exposed and the uniform membrane model of secretion given preference as compared to the dualistic model of secretion.	renewal of the agnostic position in respect of the graptolite affinity. Questions raised against Kozłowski's morphogenetic and phylogenetic theses.
PS_9	Discovery of cortical bandages (Andres, 1976, 1977 Crowther & Rickards 1977). Rejection of the membrane for a pterobranch ancestry of graptolites because of the uniformity of secretion and the similarity of structure (Crowther, 1980; Andres 1980).	modification of Kozłowski's version of the pterobranch paradigm, changing his morphogenetic and confirming his phylogenetic thesis.
PS_{10}	Discovery of a collagenous nature of the coenecium in Recent pterobranchs (Armstrong, Dilly & Urbanek 1984).	a new synthesis based on biochemical, ultrastructural and anatomical studies the revival of a modified pterobranch paradigm including the thesis on the molecular uniformity of the skeletal material.

The criticism of Kozłowski's ideas in the 1950s led to a temporary rebirth of the coelenterate paradigm within the palaeozoological – zoological community. Bohlin (1950) criticized Kozłowski's concept of the graptolite skeleton secretion and put forward again the coelenterate affinity of graptolites. Decker (1956, 1958) suggested a liberal interpretation of the preservational features recognized with what he believed to be a "higher magnification". Hyman (1959) also criticized Kozłowski in her textbook and started a chitin/protein controversy, in fact a "Scheinproblem" stemming from the imperfections of the terminology.

All this resulted in characteristically neutral or indifferent opinions regarding the systematic position of graptolites, e.g. the views of Simpson (1955) or Barrington (1965). One can regard such responses to Kozłowski's ideas and their criticism as a new problem situation (PS_6) as compared to (PS_5) which evolved right after the appearance of Kozłowski's major monograph (1949).

The inflow of new data came from the newly emerging field of palaeobiochemistry. In their studies, Foucart et al. (1964, 1965, 1966) showed the presence of aminoacids in the graptolite skeleton and provided evidence that both the pterobranchs and the graptolites have proteinaceous skeletons (PS_7).

These discoveries solved for the time being the "chitin/protein controversy" strengthening the pterobranch paradigm (PS_7).

From this stand, Kozłowski defended his theory which at that point attained the most complete expression (TT_2 of Kozłowski or TT_3'' of the pterobranch paradigm).

An attempt at testing Kozłowski's elaborate theory (TT_2) led, on the one hand, to the discovery in the graptolite skeleton of amazingly well-preserved fabrics indicative of its collagenous nature (Towe and Urbanek, 1972; Urbanek and Towe, 1974, 1975) and, on the other hand, to the recognition of a striking dissimilarity in the ultrastructure of the pterobranch and the graptolite skeleton. This may be called the discovery of an ultrastructural anomaly (PS_8). The anomaly was a puzzle from the standpoint of the close graptolite/pterobranch affinity.

The discovery of the ultrastructural anomaly would not have been possible without Dilly's (1971) excellent contribution showing the ultrastructure of the zooidal tube in the Recent *Rhabdopleura.* The same pattern was soon recognized in the Ordovician *Rhabdoplerites,* thus providing evidence of an invariable ultrastructural difference between the fusellar components of the graptolite and the pterobranch skeleton (Urbanek, 1976).

The earlier recognition of an alleged keratinous nature of the skeletal fibrils in *Rhabdopleura* also contrasted with the facts indicating the collagenous nature of the graptolite skeletal material.

The period of neo-agnosticism

This paradoxical problem situation (PS_8) brought about a revival of the agnostic approach to the graptolite affinity. The ultrastructural anomaly seemed to imply fundamental differences between the graptolites and the pterobranchs at the molecular level, undermining the earlier conviction that the microscopic resemblances between the two groups are essential. On the one hand, there was ample TEM evidence of collagenous nature of the skeletal material in graptolites, and on the other, TEM studies revealed a striking dissimilarity between the fibrous material of Pterobranchia and that of graptolites. Hence the question: is the pterobranch skeleton non-collagenous and made of keratin or of some other kind of protein?

Urbanek (1976) arrived at a conclusion that the presumed differences at the molecular level were associated with quite different modes of secretion of the skeleton in pterobranchs and in graptolites. A similar point of view was suggested, by Kirk (1972, 1974) in her evaluations of Kozłowski's and Urbanek and Towe's works.

Urbanek (1976) based his neo-agnostic approach on the contradictions exposed by him in Kozłowski's model of secretion, which was proved to be functionally impossible. He raised objections to 1) the morphogenetic thesis of Kozłowski's theory suggesting for graptolites a uniform model af secretion by a sort of membrane, 2) the phylogenetic thesis declaring the problem of graptolite affinity still unresolved and the degree of their kinship with pterobranch difficult to define.

Both points are components of what was Urbanek's new TT, a temporary solution based on the new and growing body of the ultrastructural data.

Towards a solution

Urbanek's tentative conclusion soon caused much controversy. The light microscope (Andres, 1976, 1977) and SEM studies (Crowther and Rickards, 1977) on the surface micromorphology of graptolites revealed the presence of ribbon – like units, the cortical bandages.

They were considered to be universal units of secretion of the cortical tissue, impying that the whole graptolite skeleton was secreted in the same way as that of pterobranchs.

The uniformity of secretion and the similarity of structure, two strong arguments in support of the pterobranch ancestry of graptolites, were most convincingly advanced by Crowther (1980) and created a new problem situation – (PS_9). In their highly logical inferences there was one important point which the authors brushed aside.

That was the problem of the differences at the ultrastructural level. They believed that in the future those differences would be explained somehow. But the question was how! It was clear that a number of open issues could not be solved without a better understanding of the chemical composition of the pterobranch skeleton. This was the logic of a new problem situation (PS_{10}), which developed after the essential uniformity of the mode of secretion had been established with the use the SEM techniques.

The answer has been supplied by the recent paper by Armstrong, Dilly and Urbanek (1984) on the amino-acid composition of the pterobranch skeleton. It is composed of a collagenous material with a high hydroxyproline and low hydrolysine level, although the fibrous material lacks the standard EM characteristics of collagen.

The identification of the collagenous nature of the pterobranch skeleton (PS_{10}), taken in conjunction with the presumed presence of collagen in the skeleton of fossil graptolites and with other data now supports the hypothesis that both groups are phylogenetically closely related. The proofs of this affinity can be seen in the molecular and morphogenetic uniformity, as evidenced by the TEM and chemical data on the one hand and by the LM and SEM studies on the other. The ultrastructural incongruence (revealed by the TEM technique) may be due to the remarkable polymorphism of collagen fibrils and does not contradict the close affinity between the Pterobranchia and Graptolithina.

The newly modified paradigm is a synthesis based on biochemical, ultrastructural and anatomical studies... It is a modified pterobranch paradigm which includes the thesis on morphogenetic and molecular uniformity and explains the differences at the ultrastructural level as a secondary effect of the arrangement of the tropocollagen units within the collagen fibrils.

A lesson from the debate

The long lasting phylogenetic debate on the affinities of graptolites provides a lesson to all the parties of the discussion as well as to all those engaged in phylogenetic studies. As a rule the phylogenetic conclusions are based on incomplete evidence, but striving for clarity and precision we often try to be more exact than the evidence permits and the problem requires. This is the frequent source of errors and instability of opinions.

To be more specific, I personally misunderstood the nature of the ultrastructural differences recognized between graptolites and pterobranchs, but it is also fair to say that these differences were by no means trivial. Perhaps they are among the best diagnostic features of the graptolite grade of the rhabdosome construction. The discovery of an ultrastructural anomaly, that is, of a distinct difference between the Pterobranchia and the Graptolithina in the fusellar component of their skeleton – once the source of misleading conclusions – became, however, the basis of a valuable research programme. Together with the remarkable and independent studies on the SEM micromorphology including the discovery and recognition of the morphogenetic role of the so-called cortical bandages, this research programme was instrumental in reaching a better understanding of the graptolite affinities. The graptolite workers have provided a good example of the Popperian error-elimination, a procedure which corresponds, within his scheme of Evolutionary Epistomology, to the Darwinian selection in nature that usually results in killing the unit in the competitive struggle for life. As one could expect, scientists are less moral than animals, for they "kill" (criticise and refute) only their theories. As Popper (1979: 122) puts it "Scientists try to eliminate their false theories, they try to let them die in their stead".

To be faithful to Karl Popper and to pay tribute to his popularity among naturalists in the last decades, I would quote him once more: "The difference between the amoeba and Einstein is that, although both make use of method of trial and error elimination, the amoeba dislikes to err while Einstein is intrigued by it: he consciously searches for his errors in the hope of learning by their discovery and elimination" (Popper, 1979: 70).

I feel ashamed, but I must confess that not unlike amoeba I rather dislike to err and I am intrigued more by errors of other than by my own. And this is correct – this places me somewhere between the amoeba and Einstein. But I am glad that we can learn from our mistakes and accept those theories which withstand the severe criticism best.

I am also happy to declare that it seems that as result of the growth of knowledge the graptolites have ceased to be a problematic group, but they still pose quite a few problems.

Dansk sammendrag

Debatten om graptolitternes fylogenetiske tilhørsforhold kan tjene som et eksempel, der kan underkastes en videnskabsfilosofisk analyse. Som Popper har foreslået, begynder al videnskabelig diskussion med et problem, der er blevet formuleret i sammenhæng med en situation, der har udviklet sig på grund af øget viden. Omkring 10 sådanne problemsituationer kan udskilles i den førte debat, der starter med multi-model trinnet sent i det nittende århundrede. På dette tidspunkt blev en coelenteratmodel gjort enerådende. I 1930erne kulminerede debatten ved genoplivning af klassiske forestillinger om henholdsvis tilhørsforhold til coelenterater og bryozoer. Den vigtigste nyskabelse var Kozłowski's modifikation med forslaget om en pterobranch tilknytning. De nutidige opfattelser om graptolitternes nedstamning kan direkte afledes fra Kozłowski's betydningsfulde bidrag. Nye palæontologiske resultater fra Kozłowski sammen med paleobiokemiske undersøgelser af Foucart og medarbejdere sejrede over andre opfattelser og Kozłowski's synspunkter blev almindeligt anerkendt.

Elektronmikroskopi afslørede dog betydelige forskelle mellem peridermen hos graptolitter og pterobrancher. Forskellen var vanskelig at forstå inden for Kozłowski's model og førte til et forslag om, at graptolitafstamningen stadig var et åbent spørgsmål. Imidlertid blev der påvist "cortical bandages", der pegede på et identisk mønster for sekretionen hos de to grupper. Nyere biokemiske data peger i retning af collagen-agtig substans i pterobranch skelettet, og det samme kan vises ved elektronmikroskopi hos graptolitter. Dette taler for en tæt fylogenetisk relation mellem de to grupper.

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