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THE BIOLOGY AND EVOLUTIONARY SIGNIFICANCE OF DEVONIAN VOLVOCACEANS AND THEIR PRECAMBRIAN RELATIVES

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An account of biological and evolutionary aspects of the Devonian microfossil *Eovolvor* Kaźmierczak and the related Precambrian *Eosphaera* Barghoorn is presented. New data are included confirming the volvocacean affinity of both micro-organisms along with an interpretation of reproductive cycle in the Devonian *Eovolvor*. A critical review of other volvocalean-like microfossils is also provided. Evolutionary trends in coenobial/colonial Volvocales are discussed. Comparative features of *Eovolvor* and *Eosphaera* are summarized and comments are made to the problem of the oldest eukaryotes. The significance of *Eosphaera*-like protovolvocaceans as real phyletic archetypes for early metazoans is disputed.

Key words: Volvocaceae (Phytomonadina), morphology, evolution, Devonian, Precambrian.

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INTRODUCTION

The discovery by the present writer (Kaźmierczak 1975) of a new group of fossil microorganisms closely affined to the present-day coenobial and colonial Volvocaceae (Phytomonadina) bears, somewhat unexpectedly, several important biological and geological connotations. Irrespective of their low fossilization potential, these extremely well preserved protists described as *Eovolvor silesiensis* Kaźmierczak, derived originally from Upper Devonian marine limestones drilled by a deep exploration well Sosnowiec IG 1 (Upper Silesia, southern Poland). They occur abundantly in Frasnian amphiporid pelmicrites (pl. 26: a, b) interbedded with fenestrated cryptalgal laminites. These are typical sediments for shallow-water carbonate facies of the Middle and Upper Devonian on the world scale (House 1975, for review).

The results of the present author's studies on fossil volvocaceans obtained hitherto have been presented in four reports. Two of them (Kaźmierczak 1975, 1976b) enclose besides a formal morphological description also a tentative evaluation of these fossils as paleoenvironmental indicators, and a discussion of the process of the early diagenetical calcification of their coenobia as a source of certain calcispheric structures. The other two papers (Kaźmierczak 1976a, 1979) have been devoted to the important problem of the close relationship of the Devonian volvocaceans with the problematical Precambrian microorganisms known as *Eosphaera* Barghoorn and *Eosphaera*-like sideritic microspheres, very abundant in many banded iron formations (pl. 26: c). The possibility of a direct comparison of *Eovolv vox* and *Eosphaera* seems to be of fundamental significance for the current, heated discussion (for review see: Knoll and Barghoorn 1975; Schopf and Oehler 1976; Cloud 1976; Durham 1978) on the nature and time of origin of the oldest eukaryotic organisms, and suggests that their appearance in the Earth's biosphere was much earlier than that accepted in the hypotheses existing so far.

In the opinion of many biologists, volvocaceans or related colonial flagellates were of key importance for the evolution of ancestral Metazoa and Metaphyta (e.g. Hyman 1940; Ivanov 1968). The mass occurrence of volvocaeans-like coenobial protists in the Middle Precambrian and probably even earlier appears to be a strong and real support to hypotheses deriving multicellular life from spherical colonies of diverse phyto- or zooflagellates. Therefore, one of the main aims of the present paper — besides the critical account of the results on biological significance of the fossil volvocaceans published so far — is the assessment of the evolutionary value of *Eosphaera* as possible phyletic archetypes of the simplest Metazoa.

The paper has been prepared at the Institute of Paleobiology (Zakład Paleobiologii) of the Polish Academy of Sciences in Warsaw (abbr. ZPAL), where rock samples and thin sections enclosing the Devonian volvocaceans are stored.

A REVIEW OF MICROFOSSILS OF SUPPOSED VOLVOCALEAN AFFINITY

The Devonian *Eovolv vox* Kaźmierczak and the Precambrian *Eosphaera* Barghoorn appear to be so far the only unquestionable fossil volvocaceans closely affined to members of the recent family Volvocaceae. The univocality of this relationship is documented by the presence of internal daughter coenobia in both forms which are characteristic products of vegetative reproduction in some present-day volvocaceans. However, it will be necessary to review briefly reports suggesting the presence of volvocaleans in marine and lacustrine deposits of various age and to assess critically

those fossil coenobial algae whose structure permits a comparison with volvocaceans discussed in the present paper.

The volvocacean nature was suggested by Němejc (1959) for spherical aggregates of cells occurring numerously in many limnetic Carboniferous and Permian canel and boghead coals of North America, Australia, USSR and France, and in some Lower Jurassic (Liassic) coals of France. They were described for the first time by Bertrand and Renault (1892, 1894) under the names *Pila* and *Reinschia* but no closer affiliation was proposed for them. Groups of cells observed in the thin sections within some *Pila* and *Reinschia* specimens which, in Němejc's opinion, could suggest the presence of daughter colonies characteristic of the modern *Volvox*, might well be irregular invaginations of fragments of the cell layers forming the spheroids, squeezed into their interiors as an effect of the strong compactional flattening of the material. Therefore most often *Pila* and *Reinschia* were related (e.g., Zalesskij 1914 and other authors) rather to modern coenobial Chlorococcales, particularly to various species of *Botryococcus* Kützing. In the present author's opinion the affinity of *Pila* and *Reinschia* remains still an open question and their revision is badly needed.

A volvocalean affinity was implied by De Castro (1969) for microfossils described by him as *Sgrosoella parthenopeia* from the Lower Jurassic to Upper Cretaceous marine carbonates of Italy (Campania). In De Castro's opinion *S. parthenopeia* is most similar to the modern *Prasinocladus* Kuckuck (Chlorodendrinae); the latter, however, according to the newest classifications does not belong to Volvocales but to Tetrasporales — an order of green algae enclosing forms transitional between unicellular Volvocales and coccoid Chlorococcales (e.g., Fott 1971; Round 1973; Kadłubowska 1975).

Other microfossils, known as *Thaumatoporella parvovesiculifera* (Rainer) attributed usually to dasycladaceans or red algae, are associated with *Sgrosoella parthenopeia*. According to De Castro (1969, 1975 and personal communication) they should be related rather to the extant *Volvox* Linné. However, the specimens of *Th. parvovesiculifera* illustrated so far by De Castro do not reveal clearly the presence of internal daughter colonies, he mentioned in his paper.

Sideritic microspheres similar to permineralized coenobia of *Eovolvox* and *Eosphaera* have been recently discovered by Dr. S. Kumar from the Lucknow University (personal information, April 1980) in the marine Upper Cretaceous of the Himalayas. Their potential volvocacean affinity has to be confirmed by the presence of internal structures homologous with the daughter coenobia characterizing *Eovolvox* and *Eosphaera*. If following further studies *Thaumatoporella* and the Himalayan microspheres were documented as coenobial volvocaceans their occurrence in Mesozoic marine environments, particularly common in the Upper Creta-

ceous, could be of great importance for establishing a new ecological model for the epicontinental seas they occupied.

From Upper Cretaceous sediments come also organically preserved hollow spherical cell aggregates first reported by Wetzel (1933) under the name "Morulosae" and later described by him formally as *Palambages morulosa* Wetzel, 1961. Very similar late Cretaceous microfossils were recently described as *Gambangia tremaphora* by Cookson and Eisenack (1979) from Australia. *Palambages* has a world-wide distribution and has been reported mostly from Cretaceous cherts in Europe (e.g., Górká 1963; Davey 1970; Gocht and Wille 1972), in North America (e.g., Manum and Cookson 1964; Zaitzeff and Cross 1970), in South America (Heisecke 1970) and in Australia (Cookson 1964). The detailed studies carried out by Gocht and Wille (1970) revealed that *Palambages* specimens are built of 8, 16, 32 and more cells i.e., the coenobia are formed following repeated palintomic (coupled) divisions. The lack of internal coenobia and the frequent presence of openings in the exposed external surface of each cell, demonstrated by Gocht and Wille (1970), differs *Palambages* from *Eovolv vox* and *Eosphaera* relating it to extant coenobial Chlorococcales (e.g. *Coelastrum proboscideum* Bohl.). Alternatively, *Palambages* may well be a volvoccean with an organizational grade approaching a modern *Pandorina* Bory or *Eudorina* Ehrenberg i.e., coenobial volvocaceans generating daughter aggregates within the cells of the parental coenobium. In such an interpretation the terminal openings noticed in *Palambages* by Gocht and Wille (1970) can represent perforations through which gametes, produced during the sexual phase of their life cycle, were liberated.

Fossil unicellular Volvocales (Chlamydomonadineae) are little known. Unicells described by Lignier (1906) as *Gloeocystis oxfordiensis* from the Oxfordian of France may alternatively be interpreted (Pia 1927: 56) as remnants of cyanobacterial cells. The same may be true for variously sized spherical bodies described by Edhorn (1973) as *Chlamydomonopsis primordialis* from the Precambrian Animikie rocks of Canada. Similarly, it is difficult to accept the volvoclean nature of a microfossil designated by Bradley (1946, pl. 4: 2) as *Chlamydomonas* sp. on the basis of a single specimen found in the Eocene coprolite from Wyoming. Its similarity to modern *Chlamydomonas gloeocystiformis* Dill, suggested by Bradley, is an apparent exaggeration.

The Cretaceous *Ophiobolus lapidaris* Wetzel, whose flagellum-like filament according to some authors (Wetzel 1932, 1933; Deflandre 1952; Andrews 1961) suggests their phytoflagellate affinity, have been finally recognized as microorganisms of uncertain systematic position (Wetzel 1961; Alberti 1961), most probably egg cases of some planktonic organisms (Evitt 1968).

The only satisfactorily documented fossil chlamydomonads are numerous specimens of the extant genus *Phacotus* Perty, described by Lager-

heim (1902), from the Tertiary and Quarternary lacustrine deposits of northern Europe. They are closely related to present-day *Ph. lenticularis* Ehrenberg, characterized by double calcareous tests enveloping entirely the monads.

EVIDENCES FOR THE VOLVOCACEAN AFFINITY OF THE DEVONIAN EOVOLVOX

The main morphological characteristics of *Eovolv vox* Kaźmierczak described on the basis of the type species *E. silesiensis* Kaźmierczak (mono-type) are included in an earlier paper by the present author (Kaźmierczak 1975). Features documenting the close relationship of *Eovolv vox* with the modern members of coenobial/colonial Volvocales (family Volvocaceae) will be discussed and summarized in this chapter. Comparative data on the morphology and reproduction in present-day volvocaceans have been taken mainly from the compendious works of Pascher (1927), Smith (1944), Fott (1971) and Batko (1976).

Shape and size of coenobia. — Observations of numerous *Eovolv vox* coenobia in equatorial thin sections reveal their almost ideally circular outlines (e.g., pl. 27: a, c); the subcircular and oval outlines (e.g., pl. 27: b) are the result of the compactional deformation of several specimens. A similar flattening can be observed in many spherical microfossils associated with *Eovolv vox* (e.g. in acritarchs). The size of coenobia varies in broad limits. Several hundreds of measurements show that the external diameters of coenobia are from 35 to 140 μm (ratio 1:4); about 80% of the measured specimens lie within 60—110 μm . The size ratio of *Eovolv vox* coenobia is significantly smaller than in the modern volvocacean species where size differences between young and fully grown species often approach the ratio 1:10 in non-gonidial forms (e.g. *Eudorina*) or 1:6 in gonidial forms (*Volvox* species). Similarly as in modern volvocaceans the size of *Eovolv vox* coenobia is of little diagnostic value and it is impossible to recognize any species on its basis alone.

Size and number of cells. — Size of cells in coenobial/colonial volvocaceans is not an important diagnostic feature and usually varies considerably in particular generations of one and the same species. The diameter of *Eovolv vox* cells measured at their broadest part reaches 5–27 μm and is similar to that of members of low cell-numbered modern volvocaceans (e.g. *Pandorina* Bory, *Eudorina* Ehrenberg) but much greater than that in the species of the modern *Volvox* Linné, whose cells are often below 2 μm .

It was difficult for the author to calculate the number of cells in *Eovolv vox* coenobia having only specimens in thin sections at his disposal.

Luckily, the spherical shape of coenobia permitted him to estimate the number of cells using the formula proposed by Janet (1912:28) for the calculation of cell numbers in modern spherical volvocaceans. In this formula the approximate number of cells is obtained by multiplying the square of the number of cells on a great circle by 0.367. In the case of *Evolvox* the great circle corresponds to equatorial sections of coenobia which are quite common in the studied thin sections. Since Janet's formula becomes more precise in case of colonies with cells not very apart one from the other, its application to count the tightly adhering cells forming *Evolvox* coenobia seems to be fully justified. The counts of cell numbers in 100 *Evolvox* specimens gave values varying from 49 to 522 cells divisible into four discontinuous groups:

Group	Number of counted specimens	Calculated number of cells	Mean values
(1)	6	49—69	59
(2)	17	111—139	125
(3)	48	235—271	253
(4)	29	489—522	510

The four categories of cell numbers estimated for *Evolvox* and particularly the calculated mean values prove that the coenobia have originated similarly as in most modern coenobial and colonial volvocaceans as a result of palintomic (coupled) divisions. This means that the coenobia of group (1) have been formed by six subsequent palintomic divisions producing 64 cells; those of group (2) by seven divisions producing 128 cells; those of group (3) by eight divisions producing 256 cells; and those of group (4) by nine divisions producing 512 cells. On the assumption that all counted *Evolvox* coenobia belong to one species — *E. silesiensis*, the occurrence of specimens demonstrating four orders of palintomic divisions is in agreement with the observations made on extant coenobial/colonial volvocaceans (Smith 1944; Batko 1976, for review) among which species enclosing specimens originated as a result of three, four or more orders of palintomic divisions (e.g. *Eudorina elegans* Ehrenberg, *Pandorina morum* Bory, *Volvox globator* (Linné) Ehrenberg) are known. The presence of palintomic divisions in the formation of *Evolvox* coenobia is an important diagnostic feature of these microfossils and confirms their close relationship to extant volvocaceans.

Shape and configuration of cells in coenobia. — *Evolvox* coenobia are composed of cells (monads) morphologically identical in particular specimens. Their shape is typical of monads of the present-day unicellular and coenobial/colonial Volvocales. Fig. 1 shows the main types of cell morphologies in *Evolvox* coenobia. It appears that coenobia composed of globoid (A) and ovoid (B) cells (comp. also pl. 27: b, c and pl. 29: b) are most common, whereas pyriform and spindle-shaped cells (comp. pl. 27: a) are

rarer; a few coenobia built of conoid (*D*) cells have also been found; they probably represent post mortem shrunken pyriform cells. Specimens composed of pyriform and spindle-shaped cells have as a rule a higher number of cells (usually 512, rarely 256) than those built by globoid or ovoid cells, where 512-celled aggregates are lacking. This may suggest, as it was already mentioned in an earlier paper by the present writer (Kaźmierczak

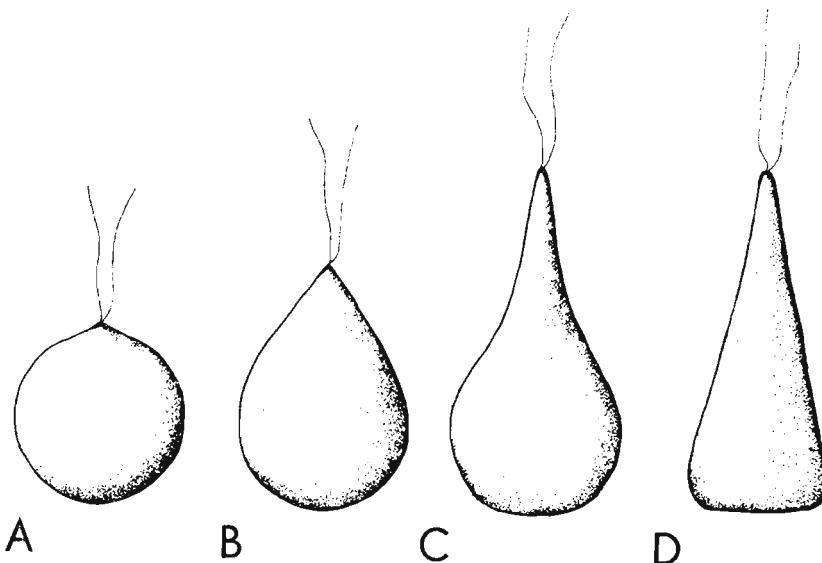


Fig. 1. Main types of cells (monads) composing coenobia of the Devonian *Eovolv vox silesiensis* Kaźmierczak (flagella reconstructed): A globoid, B ovoid, C pyriform, D conoid.

1975), that at least two coenobial morphotypes occur in *Eovolv vox silesiensis*. One of them corresponds probably to female and vegetative coenobia (aggregates built of globoid or ovoid cells), and the other to male coenobia (aggregates built of pyriform or spindle-shaped cells). However, it seems hardly justified to suggest a univocal sexual heterothallism in *E. silesiensis* because of the common post mortem deformation of their cells resulting in cell morphologies transitional between typical globoid and pyriform shapes. Generally, the range of the cell shape variation in *Eovolv vox silesiensis* is well comparable with the intraspecific variation in the cell morphology observed in recent Volvocales, particularly apparent in unicellular representatives of that group (Chlamydomonadinae).

The circular outlines of *Eovolv vox* cells in polar view and the close adherence of cells justify the supposition that the cells were not connected by cytoplasmatic strands characteristic of some members of the modern *Volvox*. Since the cells of the most modern, genuinely colonial *Volvox* species, connected by coarse cytoplasmatic strands, display a characteristic stellate shape in polar view (comp. Pascher 1927; Smith 1944), it can be

concluded that the *Evolvovox* cells, devoid of such outgrowths, were connected only by common gelatinous envelopes i.e. they represent a typical coenobial organization.

The cells of *Evolvovox* are arranged in a peripheral layer surrounding a hollow cavity. It may be supposed that similarly as in the recent *Volvox* species this cavity was to some extent filled with gelatinous substance utilized by the internally developing daughter coenobia. The gelatinous substance covered also the coenobia externally. Its presence is indirectly evidenced by the thick, early diagenetical, calcitic sheaths surrounding the coenobia. The sheaths have been formed during permineralization processes triggered off most probably by decaying gelatinous envelopes (Kaźmierczak 1976b). The closely packed cells differ *Evolvovox* from almost all high cell-numbered members of modern volvocaceans, in which cells are rather loosely distributed within the gelatinous matrix. The closely adhering cells are characteristic of some low cell-numbered non-gonidial volvocaceans like *Pandorina* Bory or the inadequately studied *Mastigospaera* Schewiakoff. In contradistinction to *Evolvovox* the central cavity in these forms is very small or entirely lacking.

Reproductive structures. — *Evolvovox* is one of a few examples of fossil protists with well preserved reproductive structures. Since these structures, known as daughter coenobia or colonies, occur only in the modern members of the family Volvocaceae they make it possible to assign directly *Evolvovox* to that group of phytoflagellates. Daughter cell aggregates are characteristic products of vegetative (asexual) reproduction in volvocaceans. In low cell-numbered (up to 128 cells) representatives of the family Volvocaceae daughter coenobia may be generated either within all the cells of a coenobium (e.g. *Gonium*) or in almost all of them (e.g. *Pleodorina*). The liberation of the very juvenile daughter aggregates is in such forms connected with the disintegration of the parental coenobium. In all species of the modern *Volvox* daughter aggregates are produced by a limited number of cells, called gonidia or eggs, which after a hypotrophic increase of their volume and a series of multiple divisions form juvenile aggregates invading the interiors of the parental structures in which they remain for a certain time. In this case the daughter aggregates leave the parents as relatively mature individuals very similar to the fully grown coenobia or colonies. Thus, the profound difference in the mode of daughter aggregate formation between various present-day volvocaceans lies in their non-gonidial or gonidial origin. The Devonian *Evolvovox* with their internally formed daughter coenobia belongs clearly to the group of gonidial volvocaceans.

The number of daughter coenobia in *Evolvovox* varies from one to five; specimens enclosing only one, or at most two, daughter coenobia are the most common (pl. 27: c; pl. 30: b). The low number of daughter coenobia in *Evolvovox* is striking when compared with the average 8—14 daughter

aggregates observed in various members of the modern *Volvox* (see Smith 1944, for review) where at most 82 daughter colonies have been observed (*Volvox gigas* Pocock). It should however, be noted that the number of daughter colonies in *Volvox tertius* Meyer, the closest of all *Volvox* species to *Evolvox* because of its relatively low number of cells (ca. 500—2,000), is significantly smaller and usually amounts from three to eight (Pocock 1938). The correlation between the number of cells in parental aggregates with the number of produced daughter structures is therefore in *Volvox* members not always positive. Certain species are known which consist of a very high number of cells (e.g. ca. 8,000—17,000-celled *V. globator*—see pl. 27: d) and produce a few daughter colonies only (usually four to seven).

The enlarged gonidial cells responsible for the creation of daughter coenobia in *Evolvox* have not been directly observed. This is understandable, since the chance to cut them accurately in a thin section was very slight because of their low number. On pl. 28: a an equatorial section of *Evolvox* coenobium is presented which encloses a small daughter structure, probably representing a strongly enlarged gonidial cell which has already invaded the interior of the parental structure since it is still surrounded by its not entirely gelatinized metaplastic wall.

Another striking feature of many *Evolvox* daughter coenobia are their large dimensions. Several examples of such structures, filling almost entirely the interiors of the parents (pl. 27: c; pl. 28: b) have been observed. This means that the liberation of *Evolvox* daughter coenobia was apparently delayed in comparison with daughter structures in the modern *Volvox* species released from the parents as relatively small bodies. Even in the case of *Evolvox* specimens containing two, three, or more daughter coenobia the latter fill usually tightly the interiors of the parents (e.g. pl. 30: b, c). Though the evacuation of daughter colonies in the modern *Volvox* can also be delayed and though up to four generations have been observed within the parental spheroid (e.g. *Volvox africana* West—see Pocock 1933), their dimensions rarely reach half those of the parents.

When several daughter coenobia occur in *Evolvox* specimens their dimensions are almost identical (e.g. pl. 30: c). This would indicate that like in many modern *Volvox* members the daughter coenobia in *Evolvox* are products of a simultaneous sequence of development. The cells of daughter coenobia in *Evolvox* are, as a rule, worse preserved than those forming the parents. Light (sparry) circular areas surrounded by sheaths of darker micrite are often the only traces recognizable in the *Evolvox* interiors as the remnants of the daughter aggregates (pl. 30: a-c). The worse preservation of daughter coenobia was most probably caused by the poorly developed metaplastic walls of their cells before evacuation from the parents, which makes them more susceptible to degradational processes.

Interpretation of the reproductive cycle in Eovolvix.—On the basis of the above observations of vegetative reproductive structures in the Devonian *Eovolvix* and the well-studied life cycles of the present-day volvocaceans (e.g. Davenport 1979, for review) it is possible to interpret the reproductive cycle of the former. The main phases of this reconstructed cycle are schematically presented on figs. 2 and 3. Fig. 2 shows the main stages of the vegetative (asexual) reproduction in *Eovolvix* enclosing: the differentiation of a gonidial cell from the morphologically identical somatic cells (*A*), its subsequent hypertrophic growth, and first palintomic divisions (*B*) resulting in the formation of a daughter coenobium invading the interior of the parental aggregate (*C*). Similarly as in the recent *Vol-*

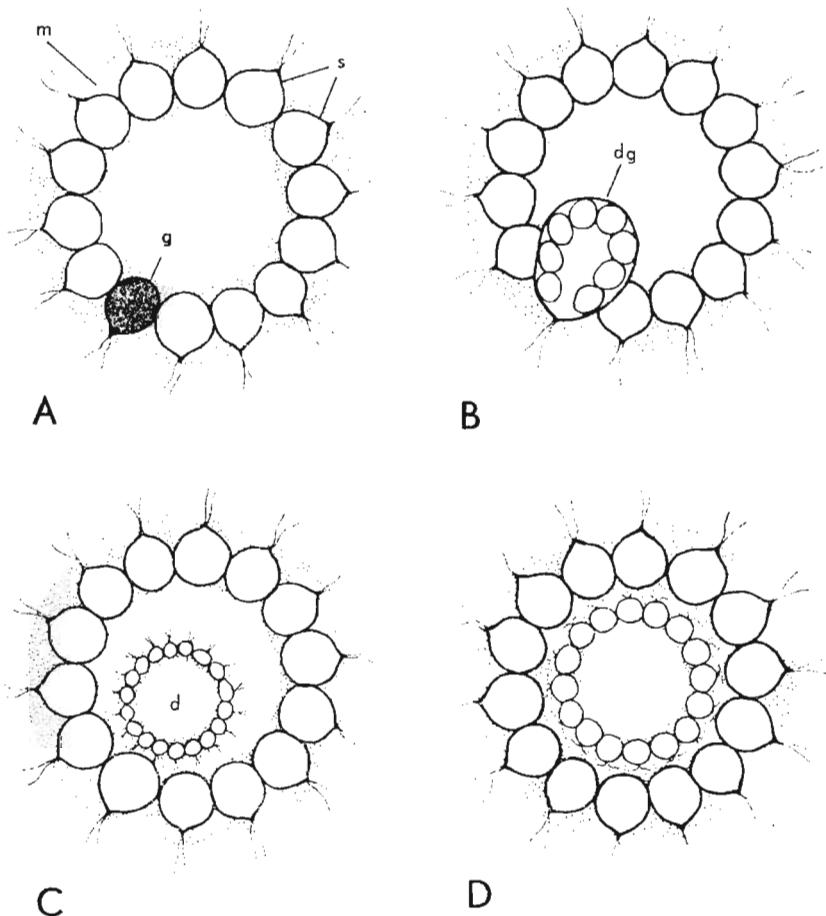


Fig. 2. A scheme illustrating the main stages of the formation of a daughter coenobium in the Devonian *Eovolvix silesiensis* Kaźmierczak: *A* differentiation of a gonidial cell (*g*) in a coenobium built of tightly adhering somatic cells (*s*) embedded in a gelatinous matrix (*m*); *B* a developing gonidial cell (*dg*) after first coupled divisions; *C* a young daughter coenobium (*d*) after inversion with outwardly exposed flagella; *D* a parental coenobium enclosing a very large daughter coenobium just before evacuation from the parental aggregate.

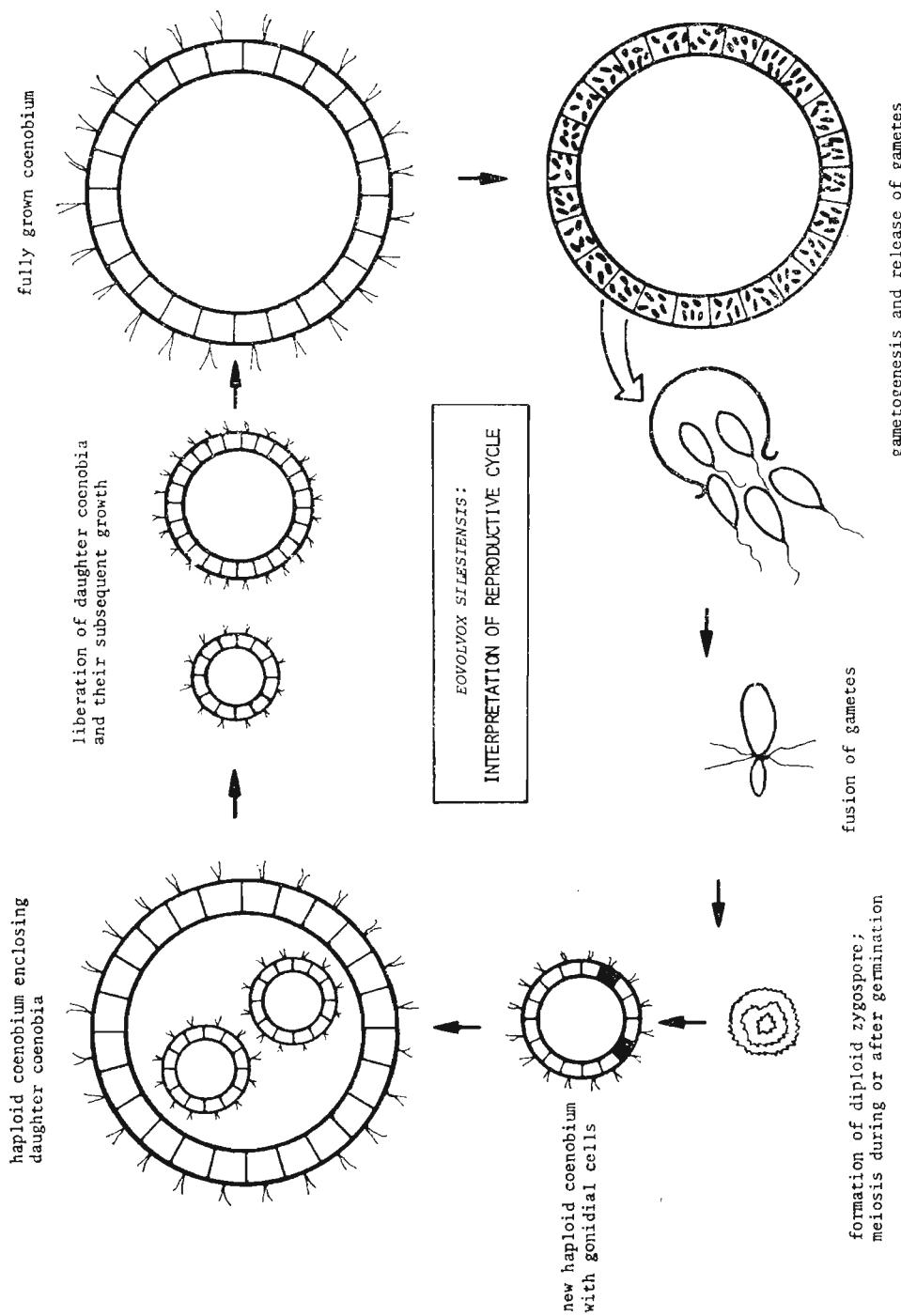


Fig. 3. For explanations see the diagram.

vox, the juvenile daughter coenobium probably became inverted and then grew up considerably, reaching often large dimensions (*D*) before leaving the parental structure. As in the modern *Volvox* the evacuation of the daughters caused disception and death of the parental aggregates.

The full reproductive cycle of *Eovolvox silesiensis* can be reconstructed as follows (fig. 3): During the asexual phase of the life cycle a haploid coenobium generated one or several gonidial cells, developing into daughter coenobia, which after the evacuation could — by generating the identically reproducing coenobia — reach the stage of a full grown aggregate with a maximal number of cells. The sexual phase was connected with the production of gametes. The lack of a morphological differentiation of cells in *Eovolvox* coenobia makes it possible to suppose that the gametes were produced by all the cells forming the aggregates. On the basis of the more or less clearly accentuated cell dimorphism (heterothallism) of *E. silesiensis* specimens mentioned before, it may be assumed that their gametogenesis was anisogamic i.e. of a kind similar to modern *Pandorina morum* or some species of *Eudorina*. This interpretation justifies the assumption that the larger and less active female gametes were produced by *Eovolvox* coenobia composed of larger and less numerous globoid or ovoid cells, whereas the smaller and highly mobile male gametes were produced by coenobia built of pyriform or spindle-shaped cells. The generation of gametes by all the cells forming the coenobia differs *Eovolvox* from modern gonidial volvocaceans, the sexual reproduction of which is oogamic in character with relatively few cells of coenobia or colonies engaged in the production of antheridial packets (males) and ova (females). Nevertheless, certain anomalies in the mode of sexual reproduction are known to occur in cultured *Volvox* species pointing to the ability to generate gametes by all the cells of the aggregates. The observations of Vande Berg and Starr (1971) which were made on usually highly cell-numbered *Volvox powersii* (Shaw) Printz well exemplify the problem. In experimental conditions the latter developed colonies of only 256 or less cells. Nearly all the cells in these forms produced egg cells (ova) and sperm packets in sexual colonies.

The alleged heterogametes produced by *Eovolvox* in sexual phase of its life cycle fused and gave rise to diploid zygospores. Knowing the details of reproduction in modern volvocaceans it may be assumed with high probability that the activated zygospores of *Eovolvox* underwent meiosis during — or shortly after — the germination and generated new haploid coenobia which eventually differentiated gonidial cells, thus beginning a new series of asexual generations.

No traces of thick-walled spiny zygospores, typical of the oogamic colonies of the modern *Volvox*, have been found in association with *Eovolvox* coenobia. This would be an additional argument for the anisogamic character of sexual reproduction in *Eovolvox*; it points out that the game-

tes copulated outside the coenobia forming zygospores which sank to the bottom. In modern *Volvox* members the resting zygotes are known to be the dominant phase in their life cycle. Although in *Eovolvovox*-bearing sediments various organically preserved spherical microfossils occur frequently, some of them very reminiscent of spiny volvocacean zygospores, to suggest their direct affiliation with *Eovolvovox* would be somewhat risky.

Biologically, the problem of single large daughter coenobia, characteristic of many *Eovolvovox* specimens and also very common in the Precambrian protovolvocaceans (*Eosphaera*) further discussed remains unclear. Although the production of singular daughter aggregates has been also accidentally observed in modern *Volvox* species (e.g. *V. amboensis* Rich and Pocock, *V. rouseletti* West — see Rich and Pocock 1933; West 1910) their very high percentage in *Eovolvovox* populations makes their effective reproductive function doubtful. Such an inefficient mode of asexual reproduction in *Eovolvovox* may suggest that the production of single daughter coenobia represented only a supplementary mode of propagation whereas the main responsibility for the population survival rested with the gametogenesis and the resulting large number of zygospores. It is highly possible that the formation of single daughter coenobia in *Eovolvovox* was more a kind of rejuvenescence of the asexual coenobia than a genuine vegetative reproduction. The biological and evolutionary implications of that intriguing phenomenon will be discussed in more details further in the text.

VOLVOCACEAN AFFINITY OF THE PRECAMBRIAN EOSPHAERA AND EOSPHAERA-LIKE STRUCTURES

The possible close relationship of the Devonian *Eovolvovox silesiensis* Kaźmierczak with the Mid-Precambrian (Gunflint Iron Fm.) *Eosphaera tyleri* Barghoorn was to some extent discussed in a previous paper by the present author (Kaźmierczak 1976a). A thorough comparison was also made by the present author (Kaźmierczak 1979) between the various preservational stages of both microorganisms recognized as *Eovolvovox* calcispheres in the shallow-water Devonian carbonates and *Eosphaera*-like sideritic microspheres commonly occurring in many Precambrian banded iron formations on the world scale (LaBerge 1967, 1973). The conclusion of these comparative studies was that the Precambrian fossils are the remnants of coenobial microorganisms, whose morphological and reproductive features link them directly with the Devonian volvocaceans and through them with some present-day volvocaceans. Volvocaceans are eukaryotic organisms and consequently the volvocacean affiliation of *Eosphaera* implies radical changes in the actually accepted model of the early biosphere evolution (Cloud 1976, Schopf 1978, for summary) and a much earlier appearance of eukaryotes than it is commonly believed (for discussion see Schopf and Oehler 1976; Cloud 1976; Francis *et al.* 1978).

The main comparative features of *Eovolvox* and *Eosphaera* are summarized below along with new data corroborating the present author's argumentation published in former papers. Abundant and variously preserved material, makes it possible to compare step by step the preservational spectra of both microorganisms beginning from organically preserved coenobia up to entirely permineralized and diagenetically altered specimens, often totally dissimilar to the initial biostructure.

The three main stages of the continuous preservational spectra of *Eovolvox* and *Eosphaera* showing their striking similarity are presented on pl. 29. Stage (1) is represented by coenobia with organically preserved cells (pl. 29: a, b), embedded in the case of *Eovolvox* in thick calcitic sheaths, and in the case of *Eosphaera* in a fine crystalline siliceous matrix. Stage (2) is shown by permineralized coenobia, in which spaces after the primary cells are still more or less recognizable (pl. 29: c, d). Such structures, though strongly differing from the organically preserved coenobia, can be still easily identified as their remnants. *Eovolvox* at this stage is represented by calcitic, irregularly double-walled spheres (pl. 29: d), and *Eosphaera* as similarly looking sideritic spheres (pl. 29: c). Stage (3) is exemplified by the remnants of permineralized coenobia with a totally obliterated biological structure; practically only the mineral sheaths, surrounding the wholly destroyed aggregates, are visible in the thin sections (pl. 29: e, f). Such structures are commonly known as sideritic, hematitic, or magnetic microspheres in the Precambrian banded iron formations (LaBerge 1967, 1973; Kaźmierczak 1979) or as some nonradiosphaerid calcspheres in the Devonian and Carboniferous shallow-water limestones (Kaźmierczak 1976b).

A comparison of organically preserved specimens of both microorganisms (Kaźmierczak 1976a) is of key importance for demonstrating the close relationship of *Eosphaera* and *Eovolvox*. This comparison shows that *Eosphaera* similarly as *Eovolvox* is a spherical aggregate of tightly adhering and peripherally distributed cells which surround a hollow cavity. The average diameters of organically preserved *Eosphaera* are significantly smaller than those of *Eovolvox* and amount, according to Barghoorn (in: Barghoorn and Tyler 1965), to 28—32 μm . However, measurements of *Eosphaera*-like structures show diameters from 24—115 μm , which are well comparable with those of *Eovolvox* (35—140 μm). Contrary to *Eovolvox* the coenobia of *Eosphaera* are composed of the globoid type of cells only. Their circular shape in polar view seems to indicate similarly as in the case of *Eovolvox* cells a lack of cytoplasmatic connections between them and consequently a typical coenobial organization of the aggregates. The calculation of cell numbers in *Eosphaera* carried out as for *Eovolvox* by means of Janet's (1912) formula gave much lower values than those for the latter. The mean values reveal the presence of 64 and 128 cells in *Eosphaera* coenobia corresponding to six and seven orders of

palintomic divisions; coenobia containing 32 cells i.e. produced by five orders of palintomy were also found in *Eosphaera*. Since the number of organically preserved *Eosphaera* described so far is rather small the calculations given above should be treated as tentative and further studies are required.

A crucial argument for determining the systematic position of *Eosphaera* is, similarly as for *Eovolv vox*, the recovery of traces of daughter coenobia within the parental aggregates. They have been found in many sideritized *Eosphaera* specimens from the banded cherts of the Gunflint Iron Formation of Canada (Kaźmierczak 1979). Their presence within the organically preserved *Eosphaera* from the typical Barghoorn's collection (*in:* Barghoorn and Tyler 1965) was also suggested earlier by the present author (Kaźmierczak 1976a). The occurrence of internal daughter coenobia in *Eosphaera* denotes that similarly as in the Devonian *Eovolv vox* and the modern *Volvox* members they have to be of gonidial origin. The striking similarity of daughter structures found in *Eosphaera*, to those from *Eovolv vox* is furthermore accentuated by their low number and large dimensions. Most of them occur singularly forming in the case of strongly permineralized coenobia a characteristic "sphere-in-sphere" pattern in thin sections (pl. 27: e, pl. 31: a-d, and Kaźmierczak 1979, fig. 3 A—C), which are identical with pictures observed in strongly permineralized *Eovolv vox* coenobia (e.g. pl. 27: f, and Kaźmierczak 1979, fig. 3 E, F). A few examples of permineralized *Eosphaera* specimens have also been found, which contain two (pl. 30: d) or three (pl. 30: e) daughter structures within the parental sphere. These have their counterparts in variously preserved *Eovolv vox* specimens illustrated in pl. 30: b, c. Although as a rule the remnants of daughter coenobia are much worse preserved than the parents, in some permineralized specimens of *Eosphaera* they reveal indistinctly preserved outlines of the primary cells (pl. 31: a, c) and it is even possible to count their numbers. For instance, the specimen of *Eosphaera*-like sideritic structure depicted in pl. 31: a contains a single daughter coenobium, built of approximately 32 cells. Typically, however, both the permineralized parent and daughter aggregates underwent strong recrystallization which made them completely dissimilar to the original organic structures (e.g. pl. 29: e; pl. 31: b, d).

From what has been said before follows that the claimed close relationship of *Eosphaera* and *Eovolv vox* seems to be fully justified. Nevertheless, further studies of organically preserved *Eosphaera* may provide new interesting details as regards these important microbiota. Such studies are actually carried out by Dr. Anna-Stina Edhorn from the Brock University, Ontario (personal information, 1980). The mineralogy of *Eosphaera*-like structures and the sedimentary features of *Eosphaera*-bearing banded iron strata have been extensively discussed by LaBerg (1967, 1973) and Kaźmierczak (1979), and need not be repeated here.

THE SIGNIFICANCE OF *EOVOLVOX* AND *EOSPHAERA* FOR THE EVOLUTION OF COENOBIAL/COLONIAL VOLVOCACEANS

The discovery of fossil volvocaceans appears to be of great significance for understanding the major evolutionary innovations occurring within this group of phytoflagellates. In evolutionary terms the present-day coenobial/colonial volvocaceans have been divided into two lineages differing apparently in the degree of the morphofunctional organization of the cell aggregates and the ontogeny structure (Batko 1976). *Eovolvvox* and *Eosphaera* occupy a very interesting position in relation to these lineages.

The first lineage is represented by coenobial cell aggregates created as a result of low order palintomic divisions of the initial monads. Such volvocaceans can be exemplified by forms with coenobia composed on average of 4—16 cells (e.g. *Gonium Müller*, *Pascherina Silva*), 16 cells (e.g. *Gonium pectorale Müller*, *Pandorina morum Bory*), 32 and 64 cells (*Eudorina Ehrenberg*, *Astrephomene Pocock*), and 128 cells (*Pleodorina californica Shaw*). The relatively large cells building such coenobia are integrated only by a common sheath of mucus and never reach the level of definitive colonies. In coenobia with less than 32 cells these are morphologically and functionally undifferentiated. Daughter coenobia generated in the vegetative phase of the life cycle are in such forms produced by all the cells composing the aggregates. Similarly, in the sexual phase of iso- or heterogamic character all cells are subjected to gametogenesis. The first differentiation of somatic and generative cells is observed starting with 32-celled coenobia. For example, in 32-celled aggregates of *Pleodorina illinoiensis Kofoid* there are four somatic cells, whereas in the 128-celled *P. californica Shaw* the somatic cells comprise half the cells of the aggregate. The somatic cells are displaced in the anterior parts of coenobia and their main function is to improve the directional locomotion of aggregates. With the development of somatic cells an axial polarity is achieved by the aggregates.

The second lineage includes forms of the broadly understood genus *Volvox* Linné, divided by Smith (1944) into four sections: *Merillosphaera*, *Copelandosphaera*, *Janetosphaera* and *Euvolvvox*. The main feature distinguishing *Volvox* members from forms of the previous lineage is a drastic reduction in the number of cells producing daughter aggregates during the vegetative phase of their life cycle. The number of these cells, called gonidia, oscillates between several and a dozen or so, and is an insignificant fraction of the total number of cells composing *Volvox* aggregates, which usually reach many thousands. The enlarged gonidial cells produce daughter aggregates invading the interiors of the parental aggregates and leaving them as relatively mature new organisms. The dramatically increased number of cells in the forms belonging to this lineage is positively correlated with the generally increasing integration of cells in aggre-

gates expressed by variously developed cytoplasmatic strands joining the cells together. They evidently improve the trophical efficiency of the multicellular structures. An increase is also noted in the volume of the gelatinous matrix surrounding the cells, which in several *Volvox* members fills also largely the interiors of colonies, serving as nutritional substance for the internally growing daughters.

The examples of *Volvox* species with a relatively low number of cells, devoid of cytoplasmatic connections, are *V. tertius* (ca 500—2,000 cells) or *V. gigas* (ca 1,000—3,000 cells) and those with a high number of cells interconnected by delicate or coarser cytoplasmatic connections *V. globator* (ca 8,000—17,000 cells) or *V. rouseletti* (ca 14,000—42,000 cells). Technical difficulties in the precise counting of cells in highly multicellular members of *Volvox* s. l. make it difficult to evaluate the final aggregates as products of palintomic (coupled) division; possibly some additional growth processes are in some forms also involved. With the increasing morphofunctional complexity and integration of cell aggregates in *Volvox* members i.e. with the transition from the coenobial to colonial organization, bearing sometimes an organismal character, the reproductive cycle is also profoundly transformed. This concerns both the asexual and sexual reproduction. The gonidial cells producing asexually daughter aggregates are larger in the less integrated systems (members of the section *Merillo-sphaera*) and their differentiation occurs early in the development of daughter aggregates (embryos). In more integrated and morphofunctionally complex colonies (sections *Janetosphaera* and *Euvolvox*) the gonidia are distinctly smaller and appear relatively late in the development of daughter colonies. The number of gonidial cells does not depend upon the degree or morphofunctional complexity of colonies and varies considerably. Similarly, the size of daughter colonies at time of their evacuation from the parental aggregates varies within broad limits (comp. data compiled by Smith 1944).

If compared with the members of the first lineage, the character of sexual reproduction in gonidial volvocaceans is deeply modified. Instead of iso- or heterogametes generated by all or many cells, in *Volvox* species relatively infrequent sexual cells are differentiated, which produce a large number of free swimming antherozoid (male cells) either by multiple divisions or by a direct enlargement giving rise to ova (female cells) retained within the colonies. Antherozoids are gathered in packets; their number varies in particular colonies from three (e.g. *V. globator*) to several hundreds (e.g. *V. gigas*). Subsequently the packets disintegrate and antherozoids swim actively to ova, which after fertilization are transformed into zygotes. The number of ova varies considerably, even within one and the same species (extremes 2—700 ova). Antheridial packets and ova may in some *Volvox* species occur jointly (monothallic species), in other species separately (heterothallic species).

The Devonian *Evolvox* and the Precambrian *Eosphaera*, because of their internal daughter coenobia, belong clearly to the lineage of gonidial volvocaceans and probably are their direct ancestors. Contrary to modern volvocaceans, living without exception in inland waters the Devonian *Evolvox* were marine plankters typical for strongly eutrophized epicontinental seas (Kaźmierczak 1975). The straight predecessors of *Evolvox* were the Precambrian *Eosphaera* which inhabited presumably also marine environments. The occurrence of internal daughter coenobia in the Mid-Precambrian volvocaceans is an evidence of a very great antiquity of gonidial volvocaceans, rooted probably in the earliest, preactualistic stages of biospheric evolution. In comparison with modern *Volvox s. l.* *Eosphaera* displays a low number of cells (usually 64 and 128, and probably also 32). The presence of daughter coenobia in *Eosphaera* indicates a very early tendency to the morphofunctional differentiation of gonidial cells in low-numbered uniform cell aggregates. A very striking feature of daughter coenobia in *Eosphaera* is their low number, in most cases it is limited to a single coenobium. As it has already been pointed out, single daughter coenobia are hardly acceptable as reproductive structures since they could not ensure the survival of the population. The origin of gonidially formed daughter aggregates should be treated rather as a sort of an evolutionary innovation at the beginning fulfilling rejuvenative function and subsequently during the further evolution of that group, overtaking the genuine reproductive function. Otherwise, as Davenport (1979) suggests, the evolutionary advantage of introducing gonidially formed daughter coenobia into the life cycle of coenobial volvocaceans might have been the isolation of reproductive cells from the mainstream of somatic function and by moving them into the interior of the parent aggregate providing them better protection. Therefore, when compared with coenobial volvocaceans creating daughter aggregates by multiple divisions of all or almost all cells forming the coenobia (e.g. *Pandorina*, *Eudorina*) and stopping for a short time their adaptive (nutritional, metabolic) activities, the gonidial volvocaceans retain during vegetative life phases their normal life functions since they already have actively living offsprings. In other words the origin of internally growing daughter aggregates may be explained as a manifestation of a tendency to autonomize the early ontogenetic stages (Batko 1976). The large dimensions of daughter coenobia in the Precambrian *Eosphaera* may be another argument indicating their initially low reproductive function. The size ratio of daughter and parental coenobia in *Eosphaera* exceeds several times the size ratios characterizing modern members of *Volvox s. l.* Single daughter coenobia in *Eosphaera* fill up almost entire interiors of the parents. This means that they have lived a relatively long time within the parents and left them as greatly efficient individuals. Since no evidence has been obtained for the existence of cytoplasmatic strands connecting the cells in *Eosphaera* and

Eovolvvox it may be assumed that the aggregates were not highly integrated.

The close similarity in the organizational pattern of *Eosphaera* and *Eovolvvox* points to a tremendous evolutionary conservatism and a high adaptability of these poorly morphofunctionally differentiated low-membered cell aggregates producing a very small number of daughter structures. Although the Devonian and Precambrian protovolvocaceans are separated by an enormous time span of about 1.5 billion years the modifications observed in *Eovolvvox* as compared with *Eosphaera* are rather insignificant. They mainly consist in the increased number of cells in *Eovolvvox* coenobia amounting usually 256, rarely 128 and 512, and exceptionally 64 cells. These values seemingly overlap the cell numbers in *Eosphaera* estimated at 64 and 128 cells. In this respect the evolutionary progress has been achieved by adding two further orders of palintomic divisions in the formation of *Eovolvvox* aggregates. A significant increase of cell sizes in the former is another progressive feature of *Eovolvvox* in comparison with *Eosphaera*. The increase in the number of cells is accompanied by the generally larger dimensions of *Eovolvvox* coenobia. An increase in the number of daughter coenobia can also be observed in *Eovolvvox*, particularly in 256- and 512-celled coenobia, which sometimes contain 3—5 daughter aggregates (pl. 28: d). In the low-numbered cell aggregates of *Eovolvvox* the tendency to produce only one large daughter coenobium characterizing *Eosphaera* is still preserved. A progressive feature of *Eovolvvox* is the appearance of at least two types of cell morphologies (globoid and pyriform) in particular coenobia, which can be interpreted as a phenotypical expression of evolutionary changes in the mode of the sexual reproduction i.e. the transition from iso- to heterogamy.

The conservative features of *Eovolvvox*, which are inherited from their *Eosphaera* predecessors and which sharply contrast them with modern *Volvox* members, are: a generally low number of cells in coenobia, lack of their morphological differentiation, low degree of aggregate integration, and lack of axial polarity, which in modern *Volvox* colonies is a manifestation of their high locomotoric abilities. A conservative feature of *Eovolvvox*, particularly interesting for understanding the evolution of the ontogeny structure in coenobial/colonial volvocaceans, is the extremely low number of daughter coenobia. In Batko's (1976) opinion the main difference between daughter structures produced in non-gonidial manner and those generated gonidially is the trophic dependence of the latter on the cells of the parental aggregate. In a different way than in non-gonidial volvocaceans, a daughter aggregate of which is a product of an individual cell and other cells of the aggregate do not participate in its formation, daughter structures in gonidial volvocaceans develop at the expense of all cells composing the parental aggregate. Until the release of the daughter the parental cells perform their normal somatic and locomotoric function,

feeding at the same time the maturing offsprings. Since in modern volvocaceans the gonidially produced daughter aggregates appear firstly in the aggregates which at least have about 500 cells, Batko (1976) assumes that this is the lowest, critical number of somatic cells able to nourish the internally growing daughter aggregates. Observations made by the present author on *Eosphaera* and *Eovolvox* modify considerably this hypothesis; he has discovered that the critical number of cells able to feed internal aggregates was much lower since such structures had already occurred in 64-celled coenobia. Nevertheless, basing on Batko's concept of the trophic dependence of the gonidially produced daughter structures on the parents, the strikingly low number of daughter coenobia in *Eosphaera* and *Eovolvox* can be easily explained. In such an interpretation it may be logically deduced that the trophic efficiency of 64- and 128-celled coenobia of *Eosphaera* and *Eovolvox* permitted them to feed most usually only one daughter structure which however continued to exploit the parental structure for a long time achieving large dimension before its evacuation. Two, three, or sometimes more daughter structures appear only in coenobia composed of 256 and 512 cells. This fact indicates a positive correlation between the number of cells in parental aggregates and the number of the produced daughter structures. It must be however noted that the number of daughter aggregates, recorded in various *Volvox* species, is not always directly related to the number of cells in parental aggregates. For instance, a particularly high humber of daughter coenobia has been observed in *V. gigas* (usually 30—60 — see Pocock 1933) and *V. powersii* (30—78 — see Pocock 1933). These values exceed several times the numbers of daughter aggregates known in other *Volvox* species. The number of cells in both species is rather small when compared with other *Volvox* members (*V. gigas*: ca 1,000—3,000 cells, *V. powersii* 1,800—2,500 cells — data after Pocock 1933) but the aggregates are characterized by very large dimensions. There is a good reason to assume that the high trophic efficiency in relation to daughter aggregates has been achieved in these forms by a very copious excretion of the gelatinous matrix into the cavity occupied by the growing daughters (comp. Vande Berg and Starr 1971).

Batko (1976), who has analyzed the continuity in the increase of the orders of palintomic divisions producing the cell aggregates in various extant Volvocales, has found an apparent lack of the 8th order of palintomy corresponding to 256-celled aggregates. Following his idea of the trophic dependence of the daughter aggregates gonidially produced from the parental aggregates Batko suggests that the 256-celled coenobia were probably insufficiently efficient trophically to evolve an ontogeny structure of the *Volvox* type. On the other hand, the development of 256-celled aggregates in volvocaceans reproducing non-gonidially was — according to this author — probably limited by the volume of the parental cells which, as indicated by the known present-day examples, could maximally

produce 128-celled daughters. The abundance of 256-celled *Evolvovox* fills Batko's gap in the continuity of palintomic spectra in Volvocales, pointing out at the same time to the high evolutionary and ecotopic adaptability of such an organizational type of volvocacean coenobia. Its long existence was probably connected with the stability of the eutrophized marine environments occupied by the Devonian volvocaceans. It may be assumed that only the later dramatic changes in the trophogenic levels of the ancient marine habitats (oligotrophication) have forced these mixotrophic protists to enter the eutrophic but otherwise unstable inland waters, where their fast specialization took place and gave rise to complex organizational patterns terminated by the present-day *Volvox* species.

In conclusion, if we take for granted that the Mid-Precambrian *Eosphaera*, the Devonian *Evolvovox* and the members of the modern *Volvox* s. l. belong to the same phylogenetic lineage of gonidial volvocaceans, the main evolutionary trends occurring during the long history of that group may be determined as follows:

- (1) Achievement during the Middle Precambrian of a coenobial organization by 5—7 orders of palintomic divisions (*Eosphaera*), with two further orders of palintomy by the Devonian time (*Evolvovox*) and several other orders later on (modern *Volvox* species);
- (2) A gradual increase in size of coenobia correlated positively with the increase of the cell number in coenobia;
- (3) A gradual increase in the number of daughter coenobia more or less positively correlated with the increasing number of cells in the parental aggregates; the increasing number of daughter coenobia is correlated with the decrease of their dimensions during evacuation from the parents;
- (4) In the sexual phase of the life cycle the transition from a supposed isogamy (*Eosphaera*) through heterogamy (*Evolvovox*) to an advanced oogamy (modern *Volvox* species);
- (5) A progressive morphofunctional differentiation of cells in aggregates and an increase of the organizational level from slightly integrated coenobia (*Eosphaera*, *Evolvovox*) to highly integrated colonies and organismal systems with cells connected by variously developed cytoplasmatic strands.

EOSPHAERA AND THE PROBLEM OF THE OLDEST EUKARYOTES

The two earlier papers by the present author (Kaźmierczak 1976a, 1979) discuss the significance of *Eosphaera* for the problem of the nature and time of origin of the oldest eukaryotes. He showed there a striking similarity of organically preserved *Eosphaera* to the evidently eukaryotic Devonian *Evolvovox* (Kaźmierczak 1976a) and an astonishing homology

between permineralized and diagenetically altered sideritized *Eosphaera* and similarly preserved calcified *Evolvox* coenobia (= volvocacean calcispheres — see Kaźmierczak 1976b, 1979). The fact of finding in the interiors of many *Eosphaera*-like sideritized structures the remnants of globular bodies displaying features that permit us to identify them with the remnants of daughter coenobia occurring in *Evolvox* was a crucial argument corroborating a close relationship between both microfossils and consequently the eukaryotic nature of *Eosphaera*. This comparison is further developed in the present paper; the author describes here *Eosphaera*-like specimens containing more than one daughter coenobium (pl. 30: d, e) and points to the presence of permineralized remnants of daughter coenobia with preserved cell outlines (pl. 31: a). All these features show that *Eosphaera* are well-established eukaryotic organisms linked with the members of the modern *Volvox* s. l. through the Devonian *Eovolvox*. It should be stressed that a direct comparison of *Eosphaera* with any living members of coenobial/colonial Volvocales would be impossible were the Devonian volvocaceans and particularly their complex preservational history not known. As it has been mentioned before the crucial evidence for the volvocacean affinity of *Eosphaera* is the presence of traces of daughter coenobia in the interiors of permineralized parental aggregates. According to the sacred principle of scientific paleontology — the rule of similarity of a fossil object to extant organisms — the gonidial volvocaceans are the only known present-day organisms reproducing by daughter aggregates formed internally. Spherical cell aggregates, occurring in cyanobacteria (*Gomphosphaeria*, *Coelosphaeridium*, *Lemmermannia*, *Marsoniella*) slightly resembling *Eosphaera* morphologically, reproduce by the ejection of single cells from the aggregates or by the disintegration of the latter. Similarly, coenobial members of chlorococcacean green algae, morphologically close to *Eosphaera*, reproduce in the asexual life phase by means of the autospores produced within each cell.

As it has been previously explained by the present author (Kaźmierczak 1976a, 1979), the presence of volvocacean-like *Eosphaera* in the ca 2 b. y. old Gunflint Iron Formation does not corroborate the commonly accepted models of the early biosphere evolution compiled by Cloud (e.g. 1972, 1976a, b) and developed by Schopf (1977, 1978, for summary). These models based on the interpretation of the Precambrian organisms so far discovered, mostly various microbiota, assume a very long prokaryotic period in the biosphere evolution enclosing the Archean and a large portion of the Proterozoic. It has been estimated that only among microfossils the age of which does not exceed 1.4—1.3 or 1.7—1.6 billion years forms comparable with modern eukaryotic cells can be identified. Some extremely sceptical opinions (e.g. Knoll and Barghoorn 1975; Francis et al. 1978) have even been voiced that the earliest appearance of eukaryotic organisms was not documented conclusively until the end of the Pre-

cambrian (the Ediacara metazoans). Others, like Edhorn (1973), Tappan (1976), Hallbauer *et al.* (1977), Pflug (1978), Pflug and Klopotek (1978), Durham 1978) argue, basing on fossil evidences, that eukaryotes may have extended appreciably further back into the Precambrian. Several authors dealing with the Precambrian microfossils avoid the problem of their biological affiliation or try to introduce parataxonomical classifications (e.g. Diver and Peat 1979 and most Soviet authors).

The biological interpretation of Precambrian microorganisms is based on the credibility of the morphological criteria used by particular authors in determining their systematic position. The taxonomic procedure is unfortunately often clouded by a great arbitrariness in the biological evaluation of morphological features observable in Precambrian microfossils. Misinterpretations of microbial contaminants and pseudofossils as primary organisms are also quite frequent (for review see Muir *et al.* 1977; Cloud and Morrison 1979).

There are four main morphological categories used commonly jointly for the assessment of the prokaryotic or eukaryotic organization in Precambrian microfossils:

- (1) cell morphologies and size ranges,
- (2) configurations of cells,
- (3) reproductive structures,
- (4) intracellular structures.

Discussion:

In reference to point (1). Schopf and Oehler (1976) tried to use cell diameters in a statistical way for separating Precambrian eukaryotes from prokaryotes. However, cell diameters alone are not an adequate criterion for claiming an eukaryotic organization because the size ranges of prokaryotic and eukaryotic cells largely overlap (prokaryotes: 0.5—55 µm, average 2—4 µm, largest 80 µm; eukaryotes: 1—350 µm, average 20 µm). Moreover, recent studies on the degradation of aggregates of coccoid cyanobacteria (Horodyski and Vonder Haar 1975; Horodyski 1980) demonstrate that often the outer sheaths of such aggregates are only preserved and leave an image of large (over 40 µm) unicells, which can be easily misinterpreted as remnants of eukaryotic cells. The cell morphology alone is of similarly little value for the assessment of pro-/eukaryotic character of the Precambrian microbiota. Most unicells have little diagnostic spherical shapes.

In reference to point (2). The cell configurations described so far or modes of cell aggregation within the Precambrian microbiota may be highly suggestive but not decisive for determining an eukaryotic organization. When used with other features like reproductive and intracellular structures cell configurations can be a valuable supporting criterion.

In reference to point (3). Reproductive structures, though unfortunately

rarely preserved, are usually a very conclusive evidence for the assessment of both prokaryotic and eukaryotic organization. For example, akinetes described in the filamentous microfossils from the Gunflint Iron Fm. (Licari and Cloud 1968) or endosporangia identified within the Late Proterozoic coccoid cell aggregates (Moorman 1974; Cloud *et al.* 1975) offer a convincing evidence for their cyanobacterial origin. Budding or cell divisions can be very similar in prokaryotic and eukaryotic unicells, therefore this criterion alone cannot be conclusive either for claiming the eukaryotic organization (e.g. for *Huroniospora* by Darby 1974, or for *Issuasphaera* by Pflug 1978) or the prokaryotic character (e.g. for Archean dyads by Knoll and Barghoorn 1977). Similarly, the various provenance of tetrahedral configurations of Precambrian cells, discussed by Oehler *et al.* (1976), may point equally to the prokaryotic or eukaryotic organization.

The best examples known so far of Precambrian microfossils with preserved reproductive structures of clearly eukaryotic type are *Ramsaysphaera* Pflug from the ca 3.4 b. y. old Swartkoppie Chert of South Africa (Pflug 1978; Pflug and Klopotek 1978), *Thuchomyces* Hallbauer and Jahns, and *Witwateromyces* Hallbauer, Jahns *et al.* Van Varmelo from the ca 2.7—2.3 b.y. old Witwatersrand Group of South Africa (Hallbauer and Van Varmelo 1974; Hallbauer *et al.* 1977), and *Eosphaera* Barghoorn from the ca. 2.0 b. y. old Gunflint Iron Formation of Canada (Barghoorn and Tyler 1965). *Ramsaysphaera* is well comparable with recent asporogenous yeasts (*Candida*) in having an almost identical morphology and mode of reproduction by multilateral budding (comp. Pflug 1978, figs. 1—2). Conidia- and sclerotia-like structures similarly well preserved, which are identified in *Thuchomyces* and *Witwateromyces* together with other morphological features, fully corroborate their close affinity with modern imperfect fungi (comp. Hallbauer *et al.* 1977, figs. 1—27). The crucial value of daughter coenobia in *Eosphaera* proving their volvocacean affinity has already been commented above.

In reference to point (4). The first attempts to interpret internal bodies ("dark spots"), occurring within some Precambrian cells as remnants of nuclei (Schopf 1968; Schopf and Blacic 1971; Schopf 1974), have been found abortive in experimental works concerned with the origin of similar structures in dehydrating cyanobacterial cells (Knoll and Barghoorn 1975; Francis *et al.* 1978). The significance of intracellular structures in Precambrian microfossils has recently been indicated in the pioneer studies of Dorothy Z. Oehler (1976, 1977). Using transmission electron micrographs of degraded recent eukaryotic algal cells for comparison she interpreted intracellular bodies occurring in some Precambrian unicells (*Glenobotrydion* Schopf) as remnants of organelles resembling pyrenoids, nuclei and chloroplasts. This very promising method is at the moment at an initial phase and, unfortunately, can be effectively applied only for an exceptionally well preserved material.

If follows from the short discussion that the idea of the long-lasting non-eukaryotic Precambrian biosphere should be seriously reconsidered. The occurrence of yeasts and lichen-like microbiota in the Archean rocks and the abundance of volvocacean-like microbiota in the banded iron formations requires a new model of the biospheric evolution which has to take into consideration the existence of at least three well-established ecosystems in the early Precambrian: (1) the stromatolitic ecosystem dominated by benthonic prokaryotes (mostly cyanobacteria), (2) the pelagic ecosystem composed of various planktonic prokaryotes and eukaryotes (yeasts in the early Archean and later phytoflagellates plus several other eukaryotic algae to be identified within the known microbiota), and (3) the semiterrestrial and ?terrestrial ecosystem represented by the lichen-like fungaceous biota from Witwatersrand.

The most recent estimations of the early Earth's oxygen budget (Schidlowski 1978) show — contrary to earlier calculations assuming a very low oxygen level during that time (e.g. Berkner and Marshall 1967; Rutten 1970; Cloud 1968) — that an early Archean oxygenic atmosphere reached probably up to 80% of the present-day oxygen level. Consequently, there are good reasons for assuming that if the benthonic stromatolitic ecosystem has probably flourished for a long time in a wholly anaerobic or only temporarily low oxygenic conditions, the two other ecosystems may well have experienced more or less oxygenic conditions well above the minimum required for an eukaryotic metabolism.

Thus, a much greater effort must be taken to discover further potential Archean eukaryotic microorganisms in non-stromatolitic rocks. The Precambrian stromatolitic communities, like their Phanerozoic counterparts, offered conditions hardly acceptable for eukaryotic life. The astronomical number of *Eosphaera*-like protovolvocaceans in the non-stromatolitic cherts of the Gunflint Iron Fm. if compared with the few specimens of that microfossils recorded by Barghoorn and Tyler (1965) and LaBerg (1973 and personal information, April 1981) from chertified stromatolitic domes is a good evidence that such a relationship exists. This means that only occasionally the planktonic *Eosphaera* and possibly other associated eukaryotic algae were post mortem entrapped by the cyanobacterial mats whereas their normal habitats were the nearby surface waters. Similar phenomenon has been observed by the present author in the distribution of the Devonian *Eovolvix* which despite their mass occurrence only exceptionally are found entombed within stromatoporoid stromatolites (= coccoid cyanobacterial mats — see Kaźmierczak 1976c, 1980, 1981) covering vast areas of the Devonian off-shore carbonate platforms.

Summing up we see that practically only the presence of characteristic reproductive structures combined in the case of multicellular forms with an intrinsic cell configuration can be a conclusive evidence of an occurrence of eukaryotic Precambrian microorganism. It should also be stressed

that the lack of positive evidence for an eukaryotic organization does not automatically imply that we have to deal with a prokaryote. This obvious fact is unfortunately not commonly considered by students interpreting the Precambrian microbiota.

EOSPHAERA AND THE ORIGIN OF MULTICELLULAR LIFE

The occurrence in the early stage of the biospheric evolution of abundant *Eosphaera*-like eukaryotic protists with an organizational grade corresponding to that of coenobial phytoflagellates leads inevitably to one of the greatest problems in biology — the origin of multicellular life. Contrary to various opinions expressed on this topic (for extensive reviews see Hyman 1940; Jägersten 1955; Hanson 1958; Greenberg 1959; Ivanov 1968; Reutterer 1969), which have been based on embryological data and theoretically deduced models, the value of the remarks presented below is that they are based on real and geologically very old paleontological objects. The occurrence of volvocacean-like protists in the evidently pre-metazoan Mid-Precambrian phase of biotic evolution offers a strong support for hypotheses suggesting that the earliest multicellular organisms are derived from variously integrated colonies of mastigophorans. The author does not propose to go into details as regards these hypotheses, broadly known as Colonial Theories, which were exhaustively reviewed by Hyman (1940) and Ivanov (1968), but would like to express his opinion that *Eosphaera* when interpreted as a volvocacean-like aggregation of flagellated cells, almost ideally fulfill the requirements formulated by Haeckel (1874) in his famous Gastraea theory of the origin of Eumetazoa for the blastaeid ancestors of premetazoans. Basing on the observations of the early developmental stages of lower metazoans (sponges and coelenterates) Hackel believed his gastraeid predecessors of the first metazoans to be hollow, spherical aggregates of undifferentiated flagellated cells comparable with present-day volvocaceans. All these features are apparently displayed by the kind of cell configuration characterizing *Eosphaera*. If so then a question arises, how good is the chance for the 32-, 64-, and 128 celled coenobia of *Eosphaera* to be accepted as a phyletic archetype of the earliest metazoans?

Before answering this question let us recall that in a common opinion (e.g. Hyman 1940; Greenberg 1959; Pantin 1960) the profound difference between colonial Protozoa and a simple many-celled animal lies in the degree of cell specialization. It has been estimated from the observations of cell specialization in the simplest extant metazoans (Greenberg 1959) that the earliest Metazoa must have been aggregations of cells of at least three to five varieties. The presence of internal daughter coenobia in *Eosphaera* — unique structures occurring only in some members of modern

volvocaceans — is a good evidence that this organism was able to produce at least three functional types of cells: (1) the flagellated somatic cells building up the parental aggregate, (2) the specialized gonidial cells differentiated from some somatic cells of the parental aggregate and responsible for the creation of daughter coenobia, and (3) the probably apochloritic, and temporally nonflagellated cells of the daughter coenobia living for some time at the expense of the parental aggregate. In other words three basic functions may be ascribed to the cells occurring within a fully developed *Eosphaera* enclosing a daughter aggregate: (1) the trophic, locomotoric and protective function of the parental cell layer responsible also for the production of gametes during the sexual life phase, (2) the reproductive function of the gonidial cells during the asexual life phase, and (3) the digestive function of the daughter cell layer nourished for some time by the parental cells.

As it has already been mentioned, the statistically very high percentage of single large daughter coenobia in *Eosphaera* makes it difficult to treat them as purely reproductive structures. Even when it is assumed that these organisms lived in highly eutrophized and void of croppers Precambrian environments (Stanley 1973), where they experienced minimum selection pressure, there is a serious doubt that single offsprings could guarantee the survival of the population. It seems quite plausible that the single daughter coenobia in *Eosphaera* have originally functioned as instruments for somatic rejuvenescence of the parental aggregates. The necessity of temporal rejuvenescence of the cell aggregates in *Eosphaera* was most probably induced by their long vegetative life phases during which the ageing cell membranes lost considerably their metabolic capability to an effective ionic exchange. It is still debatable why this somewhat curious mode of rejuvenescence was selected by the ageing coenobia instead of forming daughter aggregates within the somatic cells of the aggregates like some modern non-gonidial volvocaceans (e.g. *Pandorina*, *Eudorina*). As Davenport (1979) maintains, a reasonable answer to this question may lay in the ability developed by gonidial volvocaceans to eliminate during the formation of daughter aggregates the stage of somatic inactivity of the whole structure causing a temporal stoppage of its basic life functions. By forming daughter aggregates in a gonidial manner *Eosphaera*, like recent *Volvox* did not have to enter a non-motile condition and could pass continuously through several actively metabolizing vegetative generations. It can be logically assumed that the progenitors of *Eosphaera* were spherical, low-membered cell aggregates of modern *Pandorina* or *Mastigosphaera* type, the cells of which generated zoospores (mito-aplanospores) instead of daughter coenobia during the asexual life phase. The differentiation in such forms of the first palintomically dividing gonidial cells which opened the way to the origin of an entirely new quality — the internally growing daughter aggregates fed by the parental

coenobium — was probably impossible until a certain critical mass of cells encircling an empty cavity in such aggregates had been achieved. On the basis of the organically preserved *Eosphaera*, the lowest number of cells in an aggregate able to nourish a daughter structure can be estimated at 64 or 128 which corresponds to six and seven orders of palintomic divisions of the initial monad. When this observation is transposed to the problem of the origin of the earliest metazoans it can be expected that the 64—128-celled *Eosphaera* aggregates represent precisely the critical mass of un-specialized cells necessary for the beginning of any cell specialization.

In Severtsov's (1939) opinion the transition from palintomically produced coenobia or colonies of phytoflagellates to multicellular organisms was realized by the appearance in the ontogeny of the former of a monotomic superstructure perturbing the coupled divisions. In spherical aggregates composed of tightly adhering and peripherally distributed cells and displaying a tendency to increase the cell number, the departure from the palintomic mode of growth was indispensable for retaining the spherical geometry of the aggregate. The simplest solution in such a situation was the introduction of the monotomically produced cells into the interior of the aggregate. Following Severtsov's theory the origin of gonidial cells in *Eosphaera* may be treated as one of the first attempts of such spherical cell aggregates to depart from the inherited palintomic growth pattern. This observation together with the occurrence of the three types of functionally specialized cells in *Eosphaera* make them an exceptionally interesting model for the earliest multicellular organisms.

Embryological data collected from various eumetazoan groups show that in the most of them the first series of palintomic cleavages of an egg cell leads in a typical case (holoblastic cleavage) to the creation of a coeloblastula composed of a spherical or oval layer of cells enclosing completely a cavity known as the blastocoel. During the next stage of embryonic development a coeloblastula is converted into a gastrula by a series of cell movements perturbing the spherical geometry of the palintomically built aggregate. The process of cell movement is known as gastrulation. Gastrulation is accomplished in various ways in different groups of eumetazoans. The major types of gastrulation include:

- (1) *Invagination*, which causes a deformation of the peripheral cell layer toward the interior of the blastula; a cavity called gastrocoel is formed by such movements;
- (2) *Ingression*, by which some cells from the peripheral layer invade singly the interior;
- (3) *Delamination*, during which the inner halves of the peripheral layer are cut off by cleavage planes parallel to the surface and a more or less regular, double-layered structure is formed.

Several other modes of gastrulation are known; they are treated, however, usually as a combination of the three basic types mentioned above

(for review see: Hyman 1940; Løvtrup 1974; Seidel 1978; Davenport 1979). After completing the gastrula stage the embryos are ready to be subjected to further morphogenetic changes known as organogenesis.

The modifications occurring during the transition from the (coelo) blastula to gastrula stage are apparently associated with the loss of the palintomic division mode by the cell aggregates as was described by Svertsov (1939) for his coenobial progenitors of Metazoa. The basic product of all gastrulation types is the segregation of the increasing mass of cells of the embryo into more or less clearly defined double-layered (diploblastic) structure whose external layer is called ectoderm and internal — endoderm. It is commonly believed (see Pantin 1960, for summary) that the development of the double-layered organization was an unavoidable prerequisite in any metazoan evolution. Keeping this premise in mind we may now discuss the problem of the *Eosphaera*-like protovolvocaceans as being potential ancestors of multicellular organisms. It is rather difficult to confront directly the organizational pattern of *Eosphaera* cell aggregates with any of the types of metazoan gastrulation mentioned above. Although at the first glance the usually centrally displaced single large daughter aggregates in *Eosphaera* (fig. 4) recall diploblastic protometazoans which could have originated, according to Lankester's (1873) theory as delaminative structures, the presence of rare *Eosphaera* specimens with traces of 2—3 daughters makes such an interpretation unacceptable. The formation of gonidial cells in *Eosphaera* invading the interiors of the parental aggregates resembles very closely the ingressive type of gastrulation and may be interpreted as one of the first steps in the development of multicellular organization. The evident break of palintomic divisions in *Eosphaera*, exemplified by its gonidial cells, was only temporal in these organisms since after a short time the developing young coenobia have continued their palintomic growth pattern. The evolutionary way of *Eosphaera*-like aggregates, developing internal daughter coenobia seem to have led them therefore straight to the lineage of gonidial volvocaceans terminated through the Devonian *Eovolvvox* by the present-day *Volvox* species. Nevertheless, it may be easily accepted that perturbations in the coupled divisions of other *Eosphaera*-like Precambrian strains could also be realized otherwise. After achievement of a number of cells similar to *Eosphaera* by palintomic divisions various monotomic perturbations may have caused dramatic changes in their configuration homologous to basic gastrulation types occurring in Metazoa. Therefore *Eosphaera*-like protovolvocaceans remain valid as model organisms whose adaptive radiation could have given rise to various groups of Metazoa. A speculative protometazoan may be even proposed directly originating from those *Eosphaera*-like protovolvocaceans with single daughter coenobia (fig. 4A). Since many of such coenobia have displayed a tendency to increase their size considerably within the parental cell layer (fig. 4B) a double-layered or-

ganism could consequently originate which may resemble some diploblastic stages in metazoan embryos. Since, as it has previously been discussed, the parental cell layer was preadapted to the tropho-kinetic function and the daughter one to the digestive function, the opening of the double-layered structure, most possibly through the pressure of the increasing daughter cell layer, might itself create a Gastraea-like protometazoan (fig. 5). Such an organism could relatively easily improve its nutritional ability by using the osmotrophically active cells of the internal layer. The internal layer could have retained for some time the ability to produce its own gonidial cells, released periodically either as immature cell aggregates or enlarged egg-like asexual reproductive bodies. The opening leading to the central cavity originated probably in the weakest place of the pri-

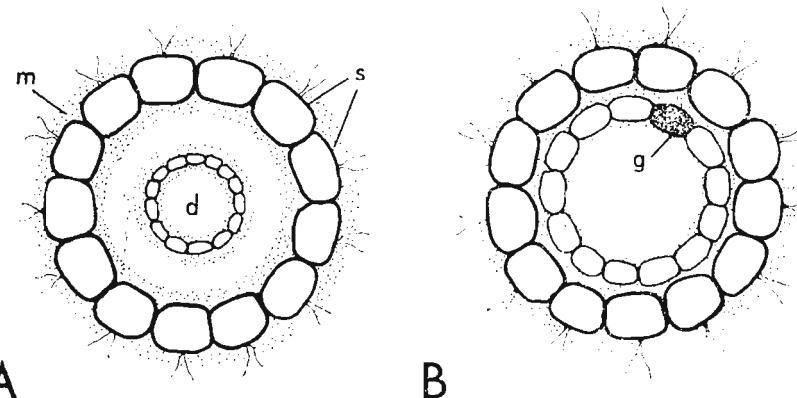


Fig. 4. Reconstructions of the two developmental stages of the Precambrian *Eosphera tyleri* Barghoorn: A a parental coenobium enclosing a young single daughter coenobium (d); B a parental coenobium enclosing a very large single daughter coenobium shortly before evacuation with an already developed gonidial cell (g).

s flagellated somatic cells, m common sheath of mucus

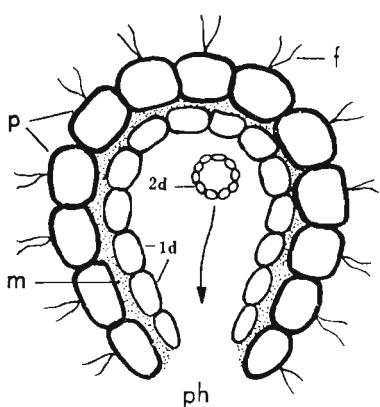


Fig. 5. An axial section of a hypothetical Gastraea-like premetazoan organism originating from *Eosphera*-like protovolvocaceans through inclusion of their single fully grown daughter coenobia in the parental aggregate; the second generation daughter structures were released either as immature coenobia or egg cells.

f flagella, m layer of the connecting mucus, p flagellated cells of the tropho-kinetic layer inherited from the parental coenobium, 1d non-flagellated cells of the digestive layer corresponding to the first generation of daughter coenobia, 2d asexual reproductive bodies (eggs) corresponding to the second generation of daughter coenobia, ph a protomouth originating from the phialopore of the parental coenobium.

mary parental cell layer corresponding to phialopore — a cross-shaped seam that commonly develops in one pole of spherical volvocacean aggregates produced by palintomic divisions.

The concept of volvocacean-like phytoflagellates as ancestral forms of multicellular organisms is not new and has its roots in the classical *Gasttraea* theory of Haeckel (1874). The *Volvox* model of early metazoans was developed particularly by Naef (1931), Severtsov (1939), Hyman (1940) and Zakhvatkin (1949). One of the main objections against this concept was a strong conviction as regards the purely autotrophic mode of nutrition of volvocaceans. In this respect non-palintomic colonies of heterotrophic flagellates similar to modern Craspedomonadina were according to some authors (e.g. Metschnikoff 1886; Ivanov 1968) more acceptable as the ancestral forms of Metozoa. However, the experimental studies of Pringsheim and Pringsheim (1959) demonstrate beyond any doubt that volvocaceans are rather distant from being obligatory autotrophs displaying without exception various kinds of mixotrophy (photoorganotrophy). These results are consistent with Pocock's (1954) studies on the African species of coenobial *Volvulina* and *Astrephomene*, which in strongly eutrophized natural waters often undergo apochlorosis and live healthy for a long time as saprophytes. The ease with which an experimental induction of apochlorosis can be obtained in laboratory-grown cultures of chromatophor-bearing flagellates, including unicellular and coenobial volvocaleans, is well documented in the literature (for review see Pringsheim 1963; DeDeken-Grenson 1959; Droop 1974). Thus, the transition from mixotrophy or saprotrophy to phagotrophy posed probably no serious problem to the protovolvocacean predecessors of Metazoa.

Finally, the idea of volvocacean predecessors of Metazoa seems to be well supported by recent studies on biochemical foundations of the origin of multicellular life. Towe (in press) following LéJohn's (1971) and Lampert's (1977) observations on the distribution of amino acids in protists and fungi concludes that only some algae (*Volvox* including) and certain fungi have an ability to synthesize hydroxyproline and hydroxylsine indispensable for the collagen production in all metazoans (Adams 1978). While both amino acids are practically absent in protozoans the derivation of the Metazoa from animal-like protists is, in Towe's opinion, hardly acceptable.

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BIOLOGIA I ZNACZENIE EWOLUCYJNE DEWOŃSKICH I PREKAMBRYJSKICH TOCZKOWCÓW (VOLVOCACEAE)

Streszczenie

Praca jest krytycznym podsumowaniem opublikowanych wcześniej rezultatów badań autora nad nową grupą mikroorganizmów kopalnych (*Eovolvox* Kaźmierczak) spokrewnionych z dzisiejszymi cenobialno-kolonijnymi wiciowcami z grupy tocz-

kowców (Volvocaceae, Phytomonadina). Organizmy te odkryte zostały w morskich osadach węglanowych górnego dewonu odwierconych na obszarze Górnego Śląska.

Dotychczasowe badania, zawarte w czterech oddzielnych pracach autora (Kaźmierzczak 1975, 1976a, b; 1979), objęły poza formalnym opisem odkrytych toczkowców, uzupełnionym obecnie o nowe szczegóły, takie zagadnienia jak: (1) znaczenie kopalnych toczkowców dla celów analizy środowiskowej, (2) wyjaśnienie niektórych dewońskich kalcyferów jako struktur powstałych w rezultacie wcześniogenetycznego otulania obumarłych cenobiów w osłonki wapienne, oraz (3) porównanie dewońskich *Eovolvovox* z enigmatycznymi mikroorganizmami prekambryjskimi znany jako *Eosphaera* Barghoorn, a także *Eosphaera*-podobnymi syderytowymi mikrosferami, występującymi masowo w obrębie prekambryjskich formacji żelazistych (tzw. dżaspitów). Zagadnienia te poszerzone są w obecnej pracy o dyskusję ewolucji struktury ontogenezy i rozmnażania wegetatywnego u cenobialno-kolonijnych toczkowców, połączona z próbą rekonstrukcji cyklu reprodukcyjnego u dewońskich prototoczkojców (*Eovolvovox*). Zestawiony został zespół cech pozwalających na bezpośredni porównanie dewońskich *Eovolvovox* ze środkowo-prekambryjskimi *Eosphaera* z formacji Gunflint w Kanadzie, wraz z komentarzem do toczącej się obecnie dyskusji nad charakterem i czasem powstania najstarszych organizmów eukariotycznych. Wskazano na znaczenie *Eosphaera* i zbliżonych mikroorganizmów prekambryjskich jako realnie istniejących filetycznych archetypów najwcześniejnych tkankowców (Metazoa). *Eosphaera* wydają się spełniać prawie idealnie warunki haeckelowskich blasteada, a ich adaptatywna radiacja mogła dać formy wyjściowe do szeregu typów Metazoa. Zaproponowano hipotetyczny typ diblastycznego mikroorganizmu jaki mógł powstać w rezultacie opóźnionego ontogenetycznego uwalniania z cenobiów macierzystych dużych, pojedyńczych cenobiów potomnych, a także, wynikający z niego model prymitywnego pratkankowca typu gastready, że szczeliną gębową powstałą w miejscu fialoporu cenobium macierzystego.

Praca została częściowo wykonana w ramach problemu MR II/6 finansowanego przez Polską Akademię Nauk.

EXPLANATION OF THE PLATES 26—31

All specimens of *Eovolvovox silesiensis* Kaźmierzczak illustrated in the plates come from the Late Devonian (Frasnian) limestone drilled by Sosnowiec IG 1 exploration well (Katowice district, southern Poland) at the depth interval of 2385—2395 m; the illustrated *Eosphaera*-like specimens derive from the Gunflint Iron Formation of Canada and were sampled at Kakabeka Falls locality, Ontario (coll. Wisconsin State University, Oshkosh). The photomicrographs have been made in transmitted plane light.

Plate 26

- a, b. *Eovolvovox*-bearing bituminous pelmicrite composed of the dense accumulations of early diagenetically calcified volvocacean coenobia and the remnants of other phytoplankters associated with amphiporid cyanobacterial stromatolites (a);

Sosnowiec IG 1 well, depth 2385—2395 m, Upper Silesia (Katowice district); Frasnian.

- c. An accumulation of *Eosphaera*-like microfossils preserved by siderite and embedded in a siliceous matrix; Kakabeka Falls (Ontario); Gunflint Iron Formation (Middle Precambrian).

Plate 27

- a, b. Two basic morphotypes of *Eovolvovox silesiensis* Kaźmierczak: a — 512-celled coenobium built of pyriform or spindle-shaped cells; b — 256-celled coenobium built of ovoid cells.
- c. An 128-celled coenobium of *E. silesiensis* enclosing very large single 64-celled daughter coenobium; the cell layers forming both coenobia almost touch each other.
- d. Recent *Volvox globator* (Linné) Ehrenberg enclosing ten daughter colonies. Note the very small size of cells building up the colony and the high number of daughter colonies as compared with *E. silesiensis*.
- e. A sideritized specimen of *Eosphaera*-like Precambrian protovolvocacean enclosing a remnant of a single daughter coenobium ("sphere-in-sphere" structure).
- f. A calcified coenobium of *E. silesiensis* with almost totally obliterated cells enclosing a daughter coenobium similarly strongly destroyed. Note the striking similarity of that microfossil with the Precambrian structures shown in e, this plate, and in plate 5.

Plate 28

Examples of *Eovolvovox silesiensis* Kaźmierczak enclosing variously preserved daughter coenobia.

- a. An obliterated ?128-celled coenobium enclosing a remnant of a small daughter aggregate probably still surrounded by the enlarged metaplastic wall of the gonidial cell.
- b. A very strongly obliterated parental coenobium encompassing a large daughter coenobium similarly badly preserved; the light sparry area, visible in the central part, delimits the interior of the daughter coenobium.
- c. An example of a well preserved 256-celled parental coenobium enclosing dispersed groups of cells representing the remnants of one or more daughter coenobia; the black rod-like objects in the close surrounding of the volvocacean represent most probably hyphae of saprophytic fungi.
- d. An ?512-celled coenobium containing two well preserved 128-celled daughter coenobia and indistinct traces of two other coenobia visible as whitish spots in the interior of the parental coenobium.

Plate 29

A comparison of variously preserved Precambrian *Eosphaera* and *Eosphaera*-like sideritic structures (left side of the plate) with similarly preserved Devonian *Eovolvovox* and volvocacean calcispheres.

- a, b. Organically preserved coenobia of (a) ?128-celled *Eosphaera* from the typical Schreiber area of the Gunflint Fm. settled in a siliceous matrix (courtesy

- Professor E. S. Barghoorn), and (b) 256-celled *Eovolv vox* embedded in a calcitic matrix.
- c, d. Permineralized coenobia of (c) *Eosphaera* (sideritized) and (d) *Eovolv vox* (calcified) with traces of primary cells visible in both specimens as irregular spaces within the mineral sheaths.
- e, f. Wholly permineralized coenobia of *Eosphaera*-like protovolvocaceans (e) compared with *Eovolv vox* (f) with totally obliterated cells; both microfossils represent and advanced stage of fossilization known in the Precambrian iron formations as ferriferous microspheres and in the Devonian as a kind of calcispheres (mainly *Vicinesphaera Antropov*).

Plate 30

Examples of homologous reproductive structures (daughter coenobia) in the Devonian *Eovolv vox* and the Precambrian *Eosphaera*-like protovolvocaceans.

- a-c. *Eovolv vox* coenobia enclosing the remnants of one (a), two (b) and three daughter coenobia (c).
- d. A wholly permineralized *Eosphaera*-like protovolvocacean with traces of similarly permineralized two daughter coenobia in the interior.
- e. Similarly preserved *Eosphaera*-like protovolvocacean (arrowed) enclosing traces of two or three daughter coenobia; the specimen below encloses an indistinct remnant of a daughter structure in the very centre.

Plate 31

Examples of sideritized *Eosphaera*-like Precambrian protovolvocaceans with remnants of daughter coenobia preserved in various ways.

- a. A strongly permineralized coenobium (arrowed) enclosing large ?32-celled coenobium in which the cell outlines are still visible.
- b. A sideritic microsphere (arrowed) enclosing a remnant of an entirely obliterated single daughter structure.
- c. An example of oxidized (?hematitized) sideritic microsphere enclosing a distinct daughter structure.
- d. A large sideritic microsphere (arrowed) encompassing traces of a double-walled daughter sphere.



