

# **How cell associations construct themselves**

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# Introduction

Constructing itself, life arranges basic chemical reactions – transcription, translation, and catalysis – in strong hierarchy of life patterns shown in the table:

Level	Life pattern ...	... is roughly equal to
4	Genome diversification network	General cell progression (living world or biosphere)
3	Genome multiplication network	Individual cell progression
2	Genome expression network	Cell
1	Gene expression network	

This hierarchy captures the immense complexity of the living world. While the genome diversification network is most likely unique, other three life patterns are enormously variable. Their innumerable variations underlie the life diversity.

To embrace life diversity, it is reasonable to have at least three taxonomic hierarchies (or genealogies): first for gene expression networks, second for genome expression networks (cells), and third for genome multiplication networks (individual cell progressions). It is important to note that, in addition to abstract taxonomic genealogies, such individual living things as gene expression networks, genome expression networks, and genome multiplication networks also arrange in concrete genealogy and that this concrete genealogy is just the genome diversification network (general cell progression). According to the nature of life patterns, this concrete genealogy is one single genealogy of genome multiplication networks at lower resolution, one single genealogy of genome expression networks at middle resolution, but a multiple  $N_1$ -fold genealogy of gene expression networks at higher resolution where  $N_1$  is a number of genes in genome of the primordial cell from which the general cell progression arose.

As soon as the coupling of genome replication to genome expression occurred for the first time, the first genome expression network emerged on the Earth. It founded the first genome multiplication network which in turn gave rise to the genome diversification network. Life history of the genome diversification network involves the evolution of genome multiplication networks creating their phylogenetic diversity. The evolution of genome multiplication networks in turn involves the evolution of genome expression networks (cells) creating their diversity too. It is reasonable to distinguish between phylogenetic and ontogenetic cell diversity. Whereas the phylogenetic cell diversity is a result of the genome multiplication and diversification during life history of the genome diversification network, the ontogenetic cell diversity is a result of differential genome expression during life history of some individual cell progressions.

Here, I review the phylogenetic cell diversity in relation to the diversity of genome multiplication networks with special focus on how cell associations construct themselves. Animal cell associations are reviewed in more details.

# Phylogenetic cell diversity

The present-day biosphere is merely a tiny slice from the living world, a visible top of iceberg in ocean of time. However, although the numbers of individual living things (gene expression networks, genome expression networks, and genome multiplication networks) in this tiny slice represents only a small fraction of the whole, it is enormous. Much work is needed to describe and systematize their diversity completely.

The origin of the first cell, the evolution of the cell types during the Life history on the Earth, and the phylogenetic relations between different cell types within the present-day biosphere remain the matter of speculations and hot debates (see, for example, Baptiste E and Brochier C 2004, Brown JR and Doolittle WF 1997, Cavalier-Smith T 1998, 2001, 2002a, 2002b, Deamer DW 1997, Emelyanov VV 2003, Gupta RS 1998, Margulis L 1996, Martin W and Russell MJ 2003, Woese CR 1998, 2000, 2002, Woese CR *et al* 2000).

The phylogenetic cell diversity can be summarized as a compact system of cell types (Table 1). To avoid confusion, an independent hierarchy of taxonomic categories is used in this system: individuals are grouped into the same shoot, shoots - into the sprig, sprigs - into the twig, and twigs - into the branch.

Table 1. System of phylogenetic cell types

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Branch 1. Bacteria
Twig 1. Unibacteria
Sprig 1. Posibacteria
Shoot 1. Actinobacteria (5 orders of individual cell progressions)
Shoot 2. Dictyoglomi (1 species of individual cell progressions)
Shoot 3. Firmicutes (3 classes of individual cell progressions)
Shoot 4. Thermotogae (7 genera of individual cell progressions)
Sprig 2. Archaeobacteria
Shoot 1. Crenarchaeota (5 orders of individual cell progressions)
Shoot 2. Euryarchaeota (8 classes of individual cell progressions)
Twig 2. Negibacteria
Sprig 1. Eobacteria
Shoot 1. Chloroflexi (6 orders of individual cell progressions)
Shoot 2. Deinococci (2 families of individual cell progressions)
Sprig 2. Glycobacteria
Shoot 1. Acidobacteria (2 families of individual cell progressions)
Shoot 2. Aquificae (2 families of individual cell progressions)
Shoot 3. Bacteroidetes (3 orders of individual cell progressions)
Shoot 4. Chlamydiae (5 families of individual cell progressions)
Shoot 5. Chlorobi (5 genera of individual cell progressions)
Shoot 6. Chrysiogenetes (1 species of individual cell progressions)
Shoot 7. Cyanobacteria (7 orders of individual cell progressions)
Shoot 8. Deferribacteres (5 genera of individual cell progressions)
Shoot 9. Fibrobacteres (3 species of individual cell progressions)
Shoot 10. Fusobacteria (7 genera of individual cell progressions)
Shoot 11. Gemmatimonadetes (1 species of individual cell progressions)
Shoot 12. Lentisphaerae (2 genera of individual cell progressions)
Shoot 13. Nitrospirae (4 genera of individual cell progressions)
Shoot 14. Planctomycetes (6 genera of individual cell progressions)

- Shoot 15. Proteobacteria (5 classes of individual cell progressions)
- Shoot 16. Spirochaetes (3 families of individual cell progressions)
- Shoot 17. Thermodesulfobacteria (3 genera of individual cell progressions)
- Shoot 18. Verrucomicrobia (2 orders of individual cell progressions)

Branch 2. Karyota

Twig 1. Unikonta

Sprig 1. Amoebozoa

- Shoot 1. Acanthamoebida (2 genera of individual cell progressions)
- Shoot 2. Entamoebida (2 genera of individual cell progressions)
- Shoot 3. Lobosea (2 orders of individual cell progressions)
- Shoot 4. Mycetozoa (5 to 8 orders of individual cell progressions)
- Shoot 5. Pelobionta (2 families of individual cell progressions)

Sprig 2. Opisthokonta

- Shoot 1. Animalia (21 to 38 phyla of individual cell progressions)
- Shoot 2. Choanoflagellata (3 families of individual cell progressions)
- Shoot 3. Fungi (4 to 5 phyla of individual cell progressions)
- Shoot 4. Microsporidia (20 to 22 families of individual cell progressions)
- Shoot 5. Nucleariida (2 genera of individual cell progressions)

Twig 2. Bikonta

Sprig 1. Cabozoa

Subsprig 1. Rhizaria

- Shoot 1. Acantharea (3 orders of individual cell progressions)
- Shoot 2. Athalamea (2 genera of individual cell progressions)
- Shoot 3. Cercozoa (3 to 9 orders of individual cell progressions)
- Shoot 4. Foraminifera (6 to 8 orders of individual cell progressions)
- Shoot 5. Haplosporidia (4 genera of individual cell progressions)
- Shoot 6. Paramyxea (2 genera of individual cell progressions)
- Shoot 7. Plasmodiophorida (7 genera of individual cell progressions)
- Shoot 8. Polycystinea (6 families of individual cell progressions)

Subsprig 2. Excavata

- Shoot 1. Diplomonadida (2 families of individual cell progressions)
- Shoot 2. Euglenozoa (7 to 9 orders of individual cell progressions)
- Shoot 3. Heterolobosea (2 orders of individual cell progressions)
- Shoot 4. Jakobidae (3 genera of individual cell progressions)
- Shoot 5. Malawimonadida (2 species of individual cell progressions)
- Shoot 6. Oxymonadida (3 families of individual cell progressions)
- Shoot 7. Parabasalida (3 orders of individual cell progressions)

Sprig 2. Corticata

Subsprig 1. Alveolata

- Shoot 1. Apicomplexa (5 to 9 orders of individual cell progressions)
- Shoot 2. Ciliophora (9 classes of individual cell progressions)
- Shoot 3. Dinoflagellata (11 to 13 orders of individual cell progressions)
- Shoot 4. Ellobiopsida (2 species of individual cell progressions)
- Shoot 5. Perkinsea (2 genera of individual cell progressions)

Subsprig 2. Plantae

- Shoot 1. Glaucophyta (5 families of individual cell progressions)
- Shoot 2. Rhodophyta (2 classes of individual cell progressions)
- Shoot 3. Viridiplantae (3 phyla of individual cell progressions)

Subsprig 3. Chromista

- Shoot 1. Actinophryida (2 genera of individual cell progressions)
- Shoot 2. Bacillariophyta (3 classes of individual cell progressions)
- Shoot 3. Bicosoecida (5 genera of individual cell progressions)
- Shoot 4. Blastocystis (6 species of individual cell progressions)
- Shoot 5. Bolidophyta (2 species of individual cell progressions)
- Shoot 6. Centrohelioczoa (3 families of individual cell progressions)
- Shoot 7. Chrysomerophyta (1 species of individual cell progressions)
- Shoot 8. Chrysophyta (6 to 9 orders of individual cell progressions)
- Shoot 9. Cryptophyta (2 to 4 families of individual cell progressions)

- Shoot 10. Developayella (1 species of individual cell progressions)
- Shoot 11. Dictyochophyta (2 orders of individual cell progressions)
- Shoot 12. Eustigmatophyta (5 genera of individual cell progressions)
- Shoot 13. Haptophyta (4 to 5 orders of individual cell progressions)
- Shoot 14. Hyphochytriomyceta (2 species of individual cell progressions)
- Shoot 15. Labyrinthulida (2 families of individual cell progressions)
- Shoot 16. Oikomonada (1 species of individual cell progressions)
- Shoot 17. Oomyceta (6 to 8 orders of individual cell progressions)
- Shoot 18. Opalinida (4 genera of individual cell progressions)
- Shoot 19. Pelagophyta (7 genera of individual cell progressions)
- Shoot 20. Phaeophyta (11 to 14 orders of individual cell progressions)
- Shoot 21. Phaeothamniophyta (2 orders of individual cell progressions)
- Shoot 22. Pinguiphyta (4 genera of individual cell progressions)
- Shoot 23. Placididea (2 genera of individual cell progressions)
- Shoot 24. Raphidophyta (5 genera of individual cell progressions)
- Shoot 25. Xanthophyta (4 orders of individual cell progressions)

Bikonta incertae sedes:

- Shoot Apusomonadida (2 genera of individual cell progressions)
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Differences between prokaryotic and eukaryotic cells with respect to spatio-temporal organization, as first defined in the 1930s by Chatton and more fully developed in the 1960s by Stanier and Van Niel, are of so profound importance and significance that systematists still prefer to claim the prokaryota-eukaryota dichotomy as the most basic in cellular world (Cavalier-Smith T 1998, Margulis L *et al* 2000, Vellai T and Vida G 1999). So, cells are usually grouped into two major taxa: Bacteria (unnecessary synonym: Prokaryota) and Karyota (unnecessary synonym Eukaryota). In system of cell types, these taxa can be ranked as branches. Which branch emerges first, Bacteria or Karyota, is unclear (Bapteste E and Brochier C 2004). Whether the first cell was a bacterium or a karyote is also not clear (Bapteste E and Brochier C 2004).

Differences between bacterial cells with a single cell membrane and cells with two concentric cell membranes are usually weighed higher than others if one wishes to divide Bacteria into separate groups (Cavalier-Smith T 1998, 2002a, Gupta RS 1998, 2000). Therefore, bacterial cells are sometimes grouped into taxa Unibacteria (synonym Monodermata) and Negibacteria (synonym Didermata) which can be ranked as twigs in separate system of cell types. Which bacterial twig emerges first, Unibacteria or Negibacteria, is unclear.

Among Unibacteria, differences in cell membrane composition give reason to recognize two large groups: Posibacteria and Archaeobacteria (Cavalier-Smith T 1998, 2002a). These taxa can be ranked as sprigs in separate system of cell types. Posibacteria usually exhibit Gram-positive staining which suggest the name of the taxon. Archaeobacteria are unique with regard to the composition of the cell membrane which is built rather by isoprenoid ether lipids than by acyl ester lipids. They are also unusual in metabolism (Schäfer G *et al* 1999). Some are known to be able to produce methane. The others are sulfate reducers. Many Archaeobacteria live in extreme environments. Some prefer habitats like geysers whose temperature exceeds that of boiling water or like black smokers with very salty, acid, or alkaline hot water. Others prefer cold habitats like glaciers. These extreme hostile conditions are unusual today but may have been prevalent on the early Earth. The question whether the earliest bacterium was a

posibacterium, an archaeobacterium or a common ancestor from which they both evolved independently is unclear at present. Posibacteria and Negibacteria are sometimes joined in a clade Eubacteria. On the contrary, Archaeobacteria and Karyota are joined in a clade Neomura. Posibacteria involve four taxa which can be ranked as shoots in separate system of cell types, Archaeobacteria - only two.

Negibacteria are characterized by secondary cell membrane and, therefore, mostly exhibit Gram-negative staining which suggest the name of the taxon (Cavalier-Smith T 1998, 2002a). Differences in the composition of the outer cell membrane allow to divide Negibacteria into two separate groups: Eobacteria and Glycobacteria. These taxa can be ranked as sprigs in separate system of cell types. In Eobacteria, both leaflets of the outer cell membrane are built by phospholipids. In Glycobacteria, the outer leaflet of the outer cell membrane is built rather by lipopolysaccharides. Since lipopolysaccharide synthesis is immensely more complex than phospholipid synthesis and is unlikely to evolve first, it is suggested that Eobacteria are more ancestral (Cavalier-Smith T 1998, 2002a). Eobacteria involve two taxa which can be ranked as shoots in separate system of cell types. Glycobacteria are more diverse and contains 18 shoots some of which tend to group with each other (for example, Bacteroidetes and Chlorobi, Chlamydiae, Lentisphaerae and Verrucomicrobia, Fibrobacteres and Acidobacteria).

At current stage, the knowledge of bacterial cell diversity in the biosphere is likely still incomplete and the list of bacterial cell types tends to lengthen (Curtis TP *et al* 2002, Hugenholtz P *et al* 1998, Rosselló-Mora R and Amann R 2001, Ward BB 2002, Whitman WB *et al* 1998, Zinder SH and Dworkin M 2001). Therefore, the system of bacterial cell types may change drastically in future.

Among Karyota, the fundamental difference between ancestrally uniciliate and biciliate cells gives reason to distinguish two large groups: Unikonta and Bikonta (Cavalier-Smith T 2002b, 2003). It is argued that the common ancestor of Unikonta probably had only a single centriole and cilium per kinetid. In some bicentriolar Unikonta, the anterior cilium remains anterior in successive cell generations and does not transform into a posterior one. On the contrary, a major shared derived character of all Bikonta is just a ciliary transformation in which the anterior cilium and its associated roots are always the first formed but, in the next cell generations, they undergo often marked changes in structure and function to become a corresponding posterior organelles. Taxa Unikonta and Bikonta can be ranked as twigs in separate system of cell types. Which karyotic twig emerges first is unclear.

Among Unikonta, two large groups can be recognized: Amoebozoa and Opisthokonta (Cavalier-Smith T 2002b, 2003). These taxa can be ranked as sprigs in separate system of cell types. Amoebozoa ancestrally had an anterior cilium. On the contrary, Opisthokonta ancestrally had a single posterior cilium with a bicentriolar kinetid. This contrasting ciliary orientation may reflect a primary divergence in feeding mode of the first karyotes. It suggests that Amoebozoa and Bikonta may be sister clades, jointly called Anterokonta. Amoebozoa involve five taxa which can be ranked as shoots in separate system of cell types, Opisthokonta - also five.

Bikonta also may be divided into two large groups: Cabozoa and Corticata (Cavalier-Smith T 2002b, 2003). In contrast to Cabozoa, Corticata have a relatively rigid cell cortex, often supported by microtubules, some of which originate as ciliary roots made of distinctive bands of aggregated microtubules, but lack evenly radiating single microtubules resembling aster. Cabozoa involve 15 taxa which can be ranked as shoots in separate system of cell types. Among Cabozoa, two subsprigs, Rhizaria (8 shoots) and Excavata (7 shoots) can be recognized. Corticata are more diverse and contains 33 shoots which may be grouped in three subsprigs: Alveolata (5 shoots), Plantae (3 shoots), and Chromista (25 shoots). The position of one bikont shoot, Apusomonadida, is unclear.

Although extremely successful due to the number of individual cell progression species, Animalia, Fungi, and Viridiplantae represent not more than only three of 59 karyotic cell types with a rank of a shoot.

In comparison with Bacteria, the knowledge of karyotic cell diversity in the biosphere is more complete, although many cell types are still poorly studied. Moreover, as last two decades show, Karyota seem to be much less diverse in terms of spatio-temporal organization of the cells than previously thought and the list of their cell types rather shortens than lengthens (Cavalier-Smith T 1998, 2002b, 2003, Corlis JO 2002, Patterson DJ 1999, Taylor FJR 2003). Therefore, the future research will undoubtedly change the system of karyotic cell types as well.

## Formation of cell associations

Since the spatio-temporal organization of individual cell progressions is much more variable than that of cells, it is not surprisingly that the diversity of individual cell progression types is enormous. This diversity depends greatly on the phylogenetic cell type (Table 1).

Here, the diversity of individual cell progressions is reviewed with special focus on formation of cell associations. Therefore, more attention is paid to phylogenetic cell types by which the formation of cell association takes place during the life history of individual cell progressions.

### A. Bacteria

In Bacteria, most individual cell progressions are characterized by dispersion of cells in environment.

However, it is now recognized that dispersed bacterial cells are often found in close association with surfaces and interfaces forming loose aggregates known as biofilms (Branda S *et al* 2005, Crespi BJ 2001, Davey ME and O'Toole GA 2000). In the nature, the biofilm usually houses a mixture of cells belonging to different individual cell progression species. Single-species biofilms are rather artificial products created for research purposes. The biofilms are as diverse as their constituent cells. The biofilm offers its member cells several benefits. Its formation and maintenance critically depends upon production of substances for exterior matrices of cells (Branda S *et al* 2005). Under different environmental conditions, the very same substances play different roles within biofilm.

Some dispersed bacterial cells have a relatively constant habitat, but others are subjected to environmental conditions that frequently change and the cell must alternate between two or many structural and functional states (Dworkin M 2001).

Additionally, in some bacterial individual cell progressions with dispersed cell arrangement, cells can closely aggregate into simplest temporary cell associations.

This modus is characteristic for proteobacterial order Myxococcales which dispersed cells live in the soil and feed on other bacteria (Dao DN *et al* 2000, Dworkin M 2001, Raven PH *et al* 1999, Zinder SH and Dworkin M 2001). In superposition of different growing individual cell progressions, the cells usually stay together in loose associations in which the digestive enzymes secreted by individual cells are pooled, thus increasing the efficiency of feeding. When nutrients are exhausted, further cell propagation is ceased and cells glide toward any aggregation centers producing numerous mounds of cells. In each mound, cells join tightly into a fruiting body, within which any cells differentiate into spores. A fruiting body is a chimerical association containing cells from different individual cell progressions. It can contain more or less elaborate stalk. The majority of the cells die in the process of forming fruiting bodies. Also in fruiting body, only spores survive and become dispersed in environment. When the conditions are more favorable, the spore germinates to continue expansion of



individual cell progression. The same individual cell progression repeatedly takes part in formation of the fruiting bodies.

Numerous bacterial individual cell progressions are characterized by formation of cell associations (Dworkin M 2001, Zinder SH and Dworkin M 2001). Bacterial primary cell colony may be formed as a cell pair, rosette, hypha, flat square, cuboid packet, clump, or sphaera. Secondary cell colony ranges from simple branching colony of hyphae to the three-dimensional mycelium.

Cell associations in form of a multinucleoid plasmodium are also known.

Unibacteria: Posibacteria: Thermotogae

In variety of Thermotogae, the progressive cell propagation is accompanied by the formation of cell pairs, hyphae, and sphaerae (Huber R and Hannig M 2003). In genus *Thermosipho*, the hypha can contain up to 12 cells surrounded by a sheath. In genus *Fervidobacterium*, the primary cell colony is either a short hypha, a small sphaera of up to 7 cells, or a large irregular aggregate of up to 50 cells.

Unibacteria: Posibacteria: Firmicutes

In variety of genera (*Bacillus*, *Clostridium*, *Desulfotomaculum*, *Sporolactobacillus*, *Sporosarcina*, *Thermoactinomyces*, etc.), the cell can change from symmetric to asymmetric cell division if conditions become hostile (Angert ER 2005, Dworkin M 2001, Errington J 2003, Zinder SH and Dworkin M 2001). During asymmetric cell division, both chromatids adopt a novel configuration stretching from the one pole of the cell to the other. The cell division machinery assembles at both poles of the cell, but cytokinesis occurs at only one pole. A portion of one chromatid is first trapped by the division septum and becomes then packaged into the smaller cell, a forespore. Daughter cells remain attached to each other forming a cell pair. The larger daughter cell, unlucky designated as mother cell, then fully encloses the forespore which differentiates into an endospore. Since the matrix of the larger cell takes part on endospore formation, the endospore has two concentric cell membranes. This condition can be a prerequisite of a negibacterial cell type origin. If the maturation of the endospore is complete, the remnant matrix of the larger cell eventually lyses and dies. The endospore is extraordinarily resistant to most external extremes (temperature, desiccation, chemical agents, radiation, physical disruption, etc.) and can remain metabolically quiescent for a considerable period of time.

In genera *Anaerobacter*, *Epulopiscium*, and *Metabacterium* (Angert ER 2005, Angert ER *et al* 1996, Angert ER and Losick RM 1998), the cell undergoes asymmetric cell division first after it contains three or more chromatids. Then, it divides at both poles so that two smaller cells are formed. They both become engulfed by the larger cell within which they propagate progressively producing multiple forespores. In *Anaerobacter* and *Metabacterium*, all forespores become mature endospores within the "mother" cell before they become released. In *Epulopiscium*, the forespores remain rather active than dormant when they become released.

In genus *Arthromitus* (Angert ER 2005), the progressive cell propagation results in formation of a long hypha attached to host ileum. Each cell within the hypha is able to undergo asymmetric cell division if environmental conditions become unfavorable. The smaller cell usually divides ones producing two identical cells which either are immediately released or become encased in a common spore coat.

In genera *Streptococcus* and *Lactobacillus*, cells are held together in hyphae (Zinder SH and Dworkin M 2001).

In genus *Sarcina*, the progressive propagation of coccoid cells results in formation of cuboid packets which in turn are held together forming a long packet chains (Zinder SH and Dworkin M 2001).

Unibacteria: Posibacteria: Actinobacteria

In Actinobacteria (Angert ER 2005, Dworkin M 2001, Raven PH *et al* 1999, Wösten HAB and Willey JM 2000), when the founder cell progressively propagates, the progeny cells remain tightly associated in a primary cell colony, forming a short hypha which then branches giving rise to a growing secondary cell colony where hyphae become more and more intricately interwoven. In genus *Streptomyces*, the secondary cell colony is distinguished by a marked tendency toward radial spreading and branching and resembles the fungal mycelium. It either penetrates into the substrate or travels along its surface. After a number of hours of substrate growth, the colony begins to develop vertically forming aerial hyphae. When conditions in environment become unfavorable, any cells in aerial hyphae differentiate into spores, which can survive even in extremely hostile conditions. Whereas other cells of the colony die rather by apoptosis, the spores are dispersed in environment. Each spore monitors its environment and, if conditions are favorable, germinates and propagates forming new primary and secondary cell colony respectively. So, spores contribute to distribution of the individual cell progression in the environment. In colony, each cell can become a new founder cell.

Negibacteria: Eobacteria: Deinococci

In Deinococcaceae (Murray RGE 1999), the cells may be held together in pairs and in tetrads.

In genus *Thermus* (Williams RAD and Da Costa MS 1999), the cells are held together in short or long hyphae. Unusual rotund forms of the primary cell colony are sometimes seen in liquid cultures. The "aggregation" type, for example, consists of several cells bound together by the external layer of the cell envelope. This layer encloses not only the cells but also a large intercellular space. A "vesicular" type is seen as developing from an extended bleb on the surface of a single cell.

Negibacteria: Eobacteria: Chloroflexi

In Chloroflexi (Hanada S and Pierson BK 2002), the cells are mostly held together in a hypha with gliding motility. In genus *Chloronema*, the hyphae are often spirally twisted

and thickly sheathed. In genus *Oscillochloris*, the hypha may be surrounded by a thin layer of slime.

Negibacteria: Glycobacteria: Aquificae

In genera such as *Aquifex*, *Hydrogenobacter*, *Hydrogenobaculum*, *Hydrogenothermus*, *Thermocrinis*, the cells may be held together in cell pairs (Huber R and Eder W 2002). Additionally, large aggregates, containing up to about 100 cells, may be formed in genera *Aquifex*, *Hydrogenothermus*, and *Thermocrinis*. Within a permanent flow of medium under exposure to air, the *in vitro* colony of the genus *Thermocrinis* grows in streamer-like cell masses predominantly composed of long hyphae.

Negibacteria: Glycobacteria: Bacteroidetes

In genus *Flexibacter* (Dworkin M 2001), the rod-shaped cell grows and undergoes progressive cell propagation producing long, threadlike hyphae. The hyphae then fragments into shorter hyphae which continue to grow and fragment. Alternatively, the hyphae can fragment into rod-shaped cells.

Negibacteria: Glycobacteria: Chlorobi

In Chlorobi (Overmann J 2000), the cells may divide by binary and ternary fission. In genus *Chloroherpeton*, the cell is a long filament, highly flexible, and motile by gliding. In genus *Chlorobium*, long chains of almost spherical cells may be formed in growing *in vitro* culture during stationary phase. Strains with vibrioid morphology can form coils of C-shaped cells. In genus *Pelodictyon*, ternary fission leads to the formation of large three-dimensional nets.

Negibacteria: Glycobacteria: Planctomycetes

In Planctomycetes (Ward N *et al* 2004), rosettes or aggregates are formed by many spherical cells joined together at the distal tips of their stalks. In genus *Isosphaera*, the cell colony is a hypha that moves by gliding.

Negibacteria: Glycobacteria: Cyanobacteria

In Cyanobacteria, the formation of cell associations is abundant (Dworkin M 2001, Meeks JC and Elhai J 2002, Raven PH *et al* 1999, Van den Hoek C *et al* 1995).

In some orders, the typical primary body plan is a hypha. In orders Oscillatoriales and Stigonematales, hypha is rather a long chain with equal diameter throughout the whole length. In order Nostocales, the hypha may be either a short trichome tapered from one end to other as in family Rivulariaceae or a long chain as much as a meter in length as in family Nostocaceae. In the hypha, cells often show signs of differentiation. In nostocaceal genus *Anabaena*, for instance, cells take on a distinctive character at regular intervals along the hypha and become able to incorporate atmospheric nitrogen into organic molecules. These few specialized cells are more larger than other cells in a hypha and have an especially thickened cell wall to maintain anaerobic conditions, since

nitrogen fixation can not occur in the presence of the oxygen. They perform nitrogen fixation for their neighbors and share the products with them. Generally, the hypha may break into fragments which separate and develop into new hyphae. Additionally, some cells in the hypha can differentiate into spores, called akinetes, which survive unfavorable environmental conditions and give rise to new hyphae contributing to the distribution of the individual cell progression in the environment (Moore D *et al* 2004). Hyphae may be dispersed in space or held together in a secondary cell colony within a thin gelatinous matrix.

In order Pleurocapsales (Angert ER 2005, Dworkin M 2001, Montejano G and León-Tejera H 2002), the cell termed a baeocyte is initially phototactic and motile by gliding until it becomes covered by a thick, fibrous sheath. At this point, the baeocyte tends to become attached to any surface and then undergoes progressive DNA replication increasing in size. In some species of genus *Dermocarpa*, the size increase is as much as 1000-fold. When the maximum size has been reached, this bacterial multinucleoid plasmodium undergoes multiple fissions within the fibrous sheath which then ruptures, releasing the numerous small baeocytes. In genus *Dermocarpella*, the growing plasmodium becomes rather ovoid and pyriform and undergoes asymmetric binary fission. The smaller portion remains attached to its original site and continues growth. The larger portion undergoes subsequent divisions to form the baeocytes. In genus *Pleurocapsa*, the growing initial plasmodium gives rise to the branching colony of plasmodia attached to each other. Each plasmodium can undergo multiple divisions to produce baeocytes.

In order Chroococcales, the primary cell colony may be either an irregular lump or a more or less accurate sphaera.

Cyanobacterial hyphae and sphaerae can control their position in the water column to obtain the optimum amount of light and nutrients.

Negibacteria: Glycobacteria: Proteobacteria

In variety of genera, the cells may be held together in cell pair, rosette, or hypha (Angert ER 2005, Dworkin M 2001, Hanson RS and Hanson TE 1996, Yurkov VV and Beatty JT 1998, Zinder SH and Dworkin M 2001).

In genus *Caulobacter* (Dworkin M 2001, Zinder SH and Dworkin M 2001), the free-swimming, non-growing, flagellate cell attaches to the substratum, takes off the flagellum, and changes to the stalked sessile stage. It then grows and divides asymmetrically producing two cells attached to each other. The bottom daughter cell, unluckily designated as mother cell, remains stalked and sessile. It will then grow to be replaced by the next cell pair. The top daughter cell produces flagellum, detaches from its sister, and become free-swimming and non-growing. It will then attach to the substratum to transform into new stalked cell, thus contributing to the distribution of individual cell progression in space. Many stalked cells may be held together in a cell colony in form of a rosette.

In genus *Bdellovibrio* (Angert ER 2005, Dworkin M 2001), the free-swimming, non-growing, flagellate cell attaches to any neighboring prey cell and penetrates its outer membrane by rapid rotation. It sheds the flagellum and enters the periplasm of the prey cell. It then grows but does not divide so that a long curved multinucleoid plasmodium is formed. Once the prey cell cytoplasm is consumed, the plasmodium ceases growth and fragments into flagellate cells. These cells then lyse the prey cell and swim off, each ready for the next encounter with a new susceptible host cell.

In genus *Rhodomicrobium* (Dworkin M 2001), the free-swimming, non-growing, flagellate cell sheds its flagellum, becomes a sessile, stalked cell, and begins to propagate progressively in the presence of optimal environmental conditions. The progeny cells remain in connection to each other forming a branching colony of hyphae. Alternatively, the colony produces both the free-swimming, non-growing, flagellate cells and spores.

Growing *in vitro* colonies of the genus *Escherichia* exhibit a complex structure with some areas undergoing cell death and reproduction being limited to a small number of cells at the colony edge (Crespi BJ 2001).

Unibacteria: Archaeobacteria: Crenarchaeota

In variety of genera, cell association occurs in form of cell pair, short hypha, or grape-like aggregate (Huber H and Stetter KO 2002). In genus *Pyrodictium*, cell association grows as a three-dimensional network of cells and extracellular hollow tubules, canulae, which interconnect the cells. In liquid cultures, the network forms flakes of up to 10 mm in diameter, visible by the naked eye, or tiny white balls about 1 mm in size.

Unibacteria: Archaeobacteria: Euryarchaeota

In variety of genera, cell association occurs in form a cell pair, tetrad, cluster, aggregate, or hypha (Bertoldo C and Antranikian G 2003, Bonin AS and Boone DR 2004, Garcia JL *et al* 2001, Whitman WB *et al* 1999, Whitman WB and Jeanthon C 2002). Hyphae differ in length.

These examples surely testify to the ability of Bacteria to exploit intercellular interactions and communication to facilitate their adaptation to changing environmental parameters.

B. Karyota

In Karyota, numerous individual cell progressions are characterized by dispersion of cells in environment.

Likewise, in some karyotic individual cell progressions with disperse cell arrangement, cells can aggregate into simplest temporary associations as well.

One example are individual cell progressions of the mycetozoal order Dictyosteliida (Cavender JC 1990, Dao DN *et al* 2000, Raven PH *et al* 1999). Two monogenomic cells

fuse and build a giant zygote which digests all the other monogenomic cells adjacent to it. When it has eaten all of them, it encysts itself in a thick wall and undergoes meiosis. Tetrads progressively propagate producing four tetradic cell progressions and then monogenomic cells are liberated from the cyst. Free monogenomic cells propagate further to continue expansion of the individual cell progression which superposes with others. When food supply is exhausted, tens of thousands of cells from different individual cell progressions join together to form moving streams of cells that converge at a central point. Here they pile atop one another to produce a conical mound called a tight aggregate. Subsequently, a tip arises at the top of this mound, and the tight aggregate bends over to produce the migrating slug with the tip of the front. The slug, also called a grex or a pseudoplasmodium, is usually 2 to 4 mm long and is encased in a slimy sheath. Moving with its anterior tip slightly raised, it migrates to leave dark and moist environment. When reaching an illuminated area, the slug ceases migration and transforms into fruiting body composed of a tubular stalk and a spore case. Within fruiting body, cells differentiate either into stalk cells or into spore cells. Whereas the spore cells disperse in environment where they can propagate further after a period of dormancy, the stalk cells inevitably die. After germination, spore can take part in growth of the individual cell progression. The same individual cell progression repeatedly takes part in formation of the fruiting bodies.

With some differences in how it occurs, this pattern of transitory cell association appears also among the heteroloboseal order Acrasida (Blanton RL 1990). In this respect, the karyotic Dictyosteliida and Acrasida resemble bacterial Myxococcales. Long treated together as cellular slime molds, Dictyosteliida and Acrasida are now recognized to be quite unrelated to each other. Although very similar, their patterns of temporal cell association seem to evolve separately.

In contrast to Bacteria, there are much more karyotic individual cell progressions which are characterized by association of the cells.

Although hypha and sphaera remain typical body plan of the primary cell colony also in Karyota, they are often more complex as in Bacteria. Some Karyota also appear to be very much better at organized division of labor in cell association. Also in Karyota, hyphae and sphaerae can form secondary cell colonies. However, karyotic secondary cell colonies are usually much more sophisticated as in Bacteria. Some colonies sustain growth perpetually, others generally have a determinate period of growth after which they maintain steady state mass.

Hyphae and sphaerae often have plasmodial character. The nuclei flow freely in plasmodium. According to the mode of formation, two types of plasmodia are usually distinguished: a coenocyte and a syncytium. A coenocyte is formed if karyokinesis is not accompanied by cytokinesis during progressive cell propagation. On the contrary, a syncytium is formed if some uninucleate cells fuse together.

Unikonta: Amoebozoa: Entamoebida

In few species of genus *Entamoeba*, immature cyst contains 1, 2, or 4 nuclei. When mature, cyst contains 8 or even 16 nuclei.

Unikonta: Amoebozoa: Lobosea

Lobosea (Goodkov AV *et al* 1999, Smirnov AV and Goodkov AV 1999) are actually plasmodia that move by means of so-called amoeboid movement and do not have constant body form. The locomotive form is the most representative characteristic. The diversity of locomotive forms is broad, but not unlimited.

In genus *Chaos* of the order Euamoebida, there are from two to several hundred nuclei per plasmodium. The plasmodium body is poly podal with strong tendency to adopt elongated form in continuous rapid locomotion. The ability to cyst formation has been reported for *Chaos illinoisense* only.

In order Leptomyxida, multinucleate plasmodia with 8 to several hundred nuclei are common. Within the plasmodium, nuclei propagate simultaneously. When fully extended, the plasmodium may be 3 mm or more in length. Cysts produced by local condensation of cytoplasm are also multinucleate. Two plasmodia merge to form a chimerical plasmodium.

In genus *Phreatamoeba*, the flattened plasmodium with a single broad pseudopodium bearing numerous subpseudopodia contains up to 40 nuclei. Plasmodia range in size from 11 to 160 mm and vary in shape from elongated to laterally expanded. Their form is irregular and changes continuously but slowly. Nuclei propagation is usually synchronous, although asynchronous propagation does occur rarely. Plasmodium fragmentation occurs independently from nuclei propagation. Cysts are spherical. By budding, the plasmodium produces flagellate uninucleate cells which swim away. The flagellate cell may also crawl across a substratum by means of temporary pseudopodia.

Unikonta: Amoebozoa: Mycetozoa

In Myxogastria (Frederick L 1990, Novozhilov YK *et al* 2000, Raven PH *et al* 1999, Sujatha A *et al* 2005), the zygote gives rise to a multinucleate plasmodium. Nuclei flow freely in the plasmodium and divide synchronously about once every 24 hours. The plasmodium creeps along and phagocytizes decaying material. Different plasmodia usually fuse to build a chimerical plasmodium which swells by further growth and becomes increasingly meshed. Cytoplasm exhibits conspicuous streaming. The plasmodium may become very large, with millions of nuclei, but ultimately, when conditions are adverse, it forms a series of small bumps, each of which becomes a fruiting body. Within the sporangium of the fruiting body, the digenomic nuclei may either become a digenomic spores or undergo meiosis. If the meiosis occurs, tetrads become immediately isolated into spores which are to be released and dispersed in environment. Inside the spore, the cell differentiates either into an amoebae-like cell or into a flagellated cell. Under favorable conditions, spore germinates and liberates mature cell. Free-living cell can repeatedly transdifferentiate, but only cells of the same differentiation type can fuse to form new zygote.

#### Unikonta: Amoebozoa: Pelobionta

In genus *Pelomyxa* (Whatley JM and Chapman-Andresen C 1990), more than a dozen of species have been described in the past, but most of them seem either to represent different stages of the life history of the same species *Pelomyxa polustris* or to be color variants of these stages resulting from the type of food. The life history begins with a small binucleate amoeboid cell. Its nuclei are large. The cell grows to a plasmodium which can contain up to 1000 or more nuclei. In plasmodium, nuclei propagate simultaneously and synchronously. While a mitotic apparatus is lacking, the nucleus simply pinches apart into two nuclei by division. During the active feeding and growth phase, the plasmodium obtains an elongated and ovoid shape and a well-developed posterior, villous uroid. Later, during the stationary phase, the plasmodium becomes spheroidal and lacks an uroid. It can either revert directly to the active stage or undergo plasmotomy to produce cysts. Cysts with two or three envelopes are also multinucleate. Large plasmodia are fragile and often fragment by binary or multiple division. In early spring, the plasmotomy gives rise to small binucleate amoeboid cells.

#### Bikonta: Cabozoa: (Rhizaria): Acantharea

In most Acantharea (Febvre J 1990), the biflagellate cell develops usually into an uninucleate amoeboid which then propagate without cytokinesis producing a multinucleate plasmodium. The plasmodium may alternate between amoeboid and radiolarian forms. A radiolarian has an elaborate mineralized skeleton composed of long spines which are distributed very regularly. The production of biflagellate cells may take place in an oval cyst after complete remodeling of plasmodium. These cells are then shed, but their fate remains unknown.

In genus *Haliommatidium*, the single nucleus does not divide during feeding and growth phase, but increases in size by progressive polyploidization. During encystment, depolyploidization occurs, abruptly restoring nuclei to a more normal size. This progressive karyokinesis is followed by fragmentation of the cytoplasm. After a series of transformation, oval flagellate cells are shed.

#### Bikonta: Cabozoa: (Rhizaria): Cercozoa

In Chlorarachniophyceae (Hibberd DJ 1990, Van den Hoek C *et al* 1995), naked amoeboid uninucleate cells are united via filopodia into net-like plasmodium. Each cell can transform itself into coccoid resting stage or produce uniflagellate zoospore. It has been suggested that resting stages appear to be able to give rise directly to the amoeboid cells and also to zoospores via tetrads. Ultimately, the zoospores appear to give rise directly to amoeboid cells.

In cercozoan genus *Cercomonas* (Mylnikov AP and Karpov SA 2004, Van den Hoek C *et al* 1995), the progressive cell propagation can be accompanied by the production of more or less flattened plasmodium with set of flagella and contractile vacuoles. Plasmodium is usually of coenocytic origin, but syncytial origin is possible too. The number of nuclei in a plasmodium may reach 100 or more. The mature plasmodium produces extensions, fragments, and disintegrates into uninucleate biflagellate cells



which can propagate further. The single cell can alternate between actively swimming stage and slightly moving trophic (amoeboid) stage. It can also encyst.

In genus *Massisteria*, the plasmodium stage is present, but cysts are not known.

In genus *Spongomonas*, biflagellate cells are embedded in common gelatinous matrix. The cell association is usually a sphaera but, sometimes, it extremely elongates into a thread-shaped mass which tends to be intricately curved. Flagella protrude to the outside of the cell association giving it a bristly appearance.

In genera *Cladomonas* and *Rhipidodendron*, biflagellate cells are embedded in a fan-shaped gelatinous matrix built of dichotomously branching gelatinous tubes which are united laterally and sometimes fuse lengthwise. In the matrix, each tube contains a single cell at its anterior end.

In desmothoracid genus *Clathrulina*, stalked cells surrounded by homogenous chitinous envelope with numerous regularly arranged openings may be associated.

In Phaeodarea (Cachon J *et al* 1990), the karyokinesis and cytokinesis are delayed so that the progressive DNA multiplication leads to the formation of an uninucleate plasmodium. Up to 2000 chromosomes may be present in the single nucleus. The plasmodium may possess an internal silica skeleton with tubular spines. Later, the plasmodium undergoes reductional karyokinesis producing hundreds of multinucleate plasmodia each of which develops two flagella.

Bikonta: Cabozoa: (Rhizaria): Foraminifera

In genus *Patellina*, the zygote propagates without cytokinesis until it becomes a plasmodium with four digenomic nuclei which then undergo meiosis. When meiosis is complete, cytokinesis occurs and all the tetrads are released from the common test. They live independently, but, soon or later, two or more cells of two mating types aggregate. In the aggregate, cells propagate without cytokinesis until they become plasmodia each with four monogenomic nuclei. Then, the plasmodia leave their tests, round out, and cytokinesis takes place producing monogenomic cells of two mating types. Whereas most of them pair and fuse to form zygotes, remaining monokaryotic cells will be later digested by zygotes which become released and live independently.

In genus *Rotaliella* (Lee JJ 1990), the zygote gives rise to a plasmodium with four digenomic nuclei. Whereas three of these nuclei remain condensed and later undergo meiosis producing twelve tetrads, the fourth nucleus does not. Instead of this, it swells, forms nucleolus, becomes active but later will die. When released from the test, tetrads live independently. After a period of growth, each tetrad propagates without cytokinesis and becomes a plasmodium with many monogenomic nuclei. When the cytokinesis occurs, monogenomic cells remain in a common test. They pair and fuse to form zygotes which become released.

In genus *Sorites*, the digenomic plasmodium contains hundreds of nuclei. Some of them become active somatic nuclei. In mature digenomic plasmodium, all nuclei undergo meiosis at the same time but tetrads from the somatic nuclei then degenerate.

In genus *Rosalina*, the digenomic plasmodium matures and produces many tetrads which then are released. Each tetrad develops its own shell and growth to monogenomic plasmodium. Mature monogenomic plasmodium undergoes cytokinesis leading to formation of gametes. In some species, gametes are flagellate and swim before fusing to form zygotes.

Generally, the plasmodium is usually surrounded by an elaborated calcareous or agglutinated test which in turn is surrounded by a network of reticulate pseudopodia. The digenomic plasmodium is usually much larger in overall size than the corresponding multinucleate plasmodium.

In genus *Syringammia* (Tendal ØS 1990), there is a plasmodium enclosed by a branched tube system made of a transparent, cement-like organic substance. Besides numerous nuclei, the cytoplasm contains huge numbers of barite crystals, granullae. The test of plasmodium consists of foreign material held together by cement-like substance. There are reasons to suppose that plasmodium is heterokaryotic with a differentiation between somatic and generative nuclei.

Bikonta: Cabozoa: (Rhizaria): Haplosporidia

Haplosporidia are symbiotrophs in invertebrate animals (Perkins FO 1990). Their life history is poorly studied. Prior to sporulation, the symbiotroph exists in host as an unwalled multinucleate plasmodium and contains haplosporosomes as the only unusual organelle. Karyokinesis occurs within a persistent nuclear envelope. Sporulation is first seen by deposition of a thin wall around the plasmodium which then becomes a sporont. Further nuclear multiplication and increase in plasmodium size is followed by multiple and irregular subdivision into uninucleate sporoblasts. It has been suggested that meiosis may occur prior to sporoblasts formation. Pairs of sporoblasts then fuse to form binucleate sporoblasts followed by karyogamy. Zygotes undergo a complex series of events to become spores. Upon degeneration of host tissue, these spores are liberated into the aqueous environment of the host. Their fate is unknown.

Bikonta: Cabozoa: (Rhizaria): Paramyxea

Paramyxea are parasites of marine invertebrate animals (Desportes I and Perkins FO 1990). The young primary cell is amoeboid. It develops between the host cells and continuously enlarges. The first karyokinesis produces two unequal nuclei. The smaller nucleus becomes surrounded by a thin layer of cytoplasm and divides to produce two equal nuclei. These nuclei then undergo propagation producing a plasmodium with a variable number of small nuclei. Propagation is accompanied by sporulation which is characterized by formation of propagules. The propagule consists of several spores enclosed inside one another that arise by a process of internal cleavage. At this stage, the plasmodium can be considered as a sporont. With increased number of nuclei, there

is increased differentiation of sporonts. In mature sporonts, some nuclei may be products of meiosis.

Bikonta: Cabozoa: (Rhizaria): Plasmodiophorida

Plasmodiophorida are symbiotrophs of plants, fungi, etc. (Dylewski DP 1990). The biflagellate cell infects the host cell and develops into the spherical multinucleate plasmodium. At the cessation of nuclei propagation, cleavage by furrowing occurs correlated closely with the meiosis. The karyogamy has also been claimed to occur. The cleavage results in production of spores which develops in biflagellate cells infecting new hosts.

Bikonta: Cabozoa: (Rhizaria): Polycystinea

In Polycystinea (Cachon J *et al* 1990), the karyokinesis and cytokinesis are delayed so that the progressive DNA multiplication leads to the formation of an uninucleate plasmodium. During this growth phase, the nucleus increases progressively in size becoming huge in some genera (for example, *Thalassicolla*). The plasmodium is characterized by regularly perforated internal silica skeleton with radial axopods emerging among fine, ramified pseudopods. Later, the plasmodium undergoes division by binary fission, multiple fission, or budding. Division of the nucleus differs from typical mitosis in several respects. Multiple fission is thought to involve depolyploidization, since the number of chromosomes decreases at each successive division until small biflagellate spores are formed, each only with few chromosomes. Spores are formed inside the original central capsule. They may be released directly into the surrounding water after the capsule bursts. The capsule formation may be also associated with the development of the special polycystarian stage. Triggered by an unknown cause, the capsule flattens, widens, and lengthens into long tubes that give rise to small capsules from which the spores are then liberated.

In genus *Collozoum*, for example, there are large associations of shelled plasmodia which are held together by a gelatinous matrix.

Bikonta: Cabozoa: (Excavata): Diplomonadida

In order *Giardia* (Adam RD 2001, Svärd SG *et al* 2003, Vickerman K 1990a, Yu LZ *et al* 2002), the trophozoite is a plasmodium which contains two digenomic nuclei. The trophozoite can be considered a bitygote. Within the plasmodium, nuclei replicate synchronously and the fundamental task of the cytokinesis is to make sure that the nuclei are distributed to the daughter plasmodia accurately. Upon induction of encystation, the trophozoite quickly becomes rounded and both nuclei replicate. Late in encystation, the karyokinesis occurs and four nuclei replicate, generating plasmodium with four digenomic nuclei each of which is tetraploid. If released from the cyst, the plasmodium becomes an excyzoite which undergoes twice the cytokinesis and four trophozoites are formed. The cytokinesis in the excyzoite is reminiscent of meiosis and syngamy. However, whether it is an ancestral or derivative form of them is still not clear.

Bikonta: Cabozoa: (Excavata): Euglenozoa

Euglenozoa can give rise to very dense population, causing water blooms (Van den Hoek C *et al* 1995). Cells lose their flagella, surround themselves in a thick envelope of mucilage, and cover the surface of the water with a floating skin (for example, euglenid genus *Euglena*).

In genus *Colacium* (Walne PL and Kivic PA 1990), cell association is made up of two to eight stalked cells enclosed in mucilaginous envelopes. Cells may redevelop flagella, swim away from colony, settle elsewhere eventually on their anterior ends, and secrete new stalks to form new colonies.

In genus *Cephalothamnium* of the order Kinetoplastida (Vickerman K 1990b), cells are clustered at the end of a common secreted stalk which is attached to the copepod host. Flagellated cells are attached to the stalk by their posterior ends.

Bikonta: Cabozoa: (Excavata): Oxymonadida

In some Oxymonadida, cell associations in form of a multinucleate plasmodium may occur.

Bikonta: Cabozoa: (Excavata): Parabasalida

In Calonymphyda (Dolan MF *et al* 2000, Dyer BD 1990b), nuclei propagation leads to formation of a plasmodium. In plasmodium, the number of parabasal bodies, axostyles, and cilia seems to be multiplied in proportion to the number of nuclei. In genus *Metacoronymph*, for example, the plasmodium may contain as many as 1000 nuclei. The plasmodium frequently divides symmetrically or asymmetrically producing smaller plasmodia.

Bikonta: Corticata: (Alveolata): Apicomplexa

Apicomplexa are parasites of animals (Vivier E and Desportes I 1990).

In class Gregarina, the spherical mature gamontocyst contains numerous spindle-shaped young sporocysts each of which is occupied by a zygote. The zygote immediately undergoes meiosis and tetrads then divide one time so that the mature sporocyst contains eight sporozoites. When released from the gamontocyst, each sporocyst can infect a new host and liberate sporozoites. If the single sporozoite enters a host cell, it propagates producing many merozoites. Some of the merozoites transform into gamonts. Two gamonts pair, join together, and become surrounded by a common cyst wall forming a young gamontocyst within which both gamonts propagate without cytokinesis producing two multinucleate plasmodia. In each plasmodium, nuclei travel to the periphery where the cytokinesis occurs producing numerous gametes. The remainders of plasmodia perish. Within the common gamontocyst, gametes pair and fuse to produce zygotes each of which become surrounded by separate cyst wall forming new sporocyst.

Bikonta: Corticata: (Alveolata): Ciliophora

Traditionally, Ciliophora are treated as a single-celled (Dovgal IV 2002, Fokin SI *et al* 2001, Lynn DH and Small EB 1990, Orias E 1998). But actually, they are motile multinucleate plasmodia. The plasmodium typically has a large number of characteristic cilia which are arranged in longitudinal rows or spirals. Coordinated beating of cilia provides motility to plasmodium. Cilia often fuse to form structures specialized for feeding or locomotion. Food enters through gullet and passes in specialized vacuoles. Waste products empty via cytoproct. Plasmodium usually releases tough but flexible outer pellicle.

In genus *Paramecium*, for instance, the zygote progressively propagates without cytokinesis producing a plasmodium with four digenomic nuclei. Cytokinesis yields two dikaryotic plasmodia. In each of them, one nucleus differentiates into a large macronucleus which swells, forms nucleolus, and makes the plasmodium metabolically active. The other nucleus undergoes mitosis to form two digenomic nuclei, micronuclei, which remain condensed and inactive. The trikaryotic plasmodium can move as a whole by numerous cilia. It contains some differently specialized regions. Plasmodium can divide by transverse fission. It can also encyst to disperse in environment. When the time is ripe, micronuclei undergo meiosis to produce monogenomic nuclei, of which all but one degenerate. The macronucleus degenerates too. Remaining monogenomic nucleus divides once more to produce two nuclei. One of them remains stationary but the other becomes migratory. The nuclei pair and fuse to form a new digenomic nucleus and the cell becomes a zygote. Often, the production of the stationary and migratory nuclei is accompanied by conjugation of two trikaryotic plasmodia whereby they form a cytoplasmic bridge and can exchange the migratory nuclei. Each migratory nucleus crosses the cytoplasmic bridge, pairs and fuses with a stationary nucleus of the conjugation partner. Both plasmodia become zygotes which then separate from each other.

In *Tetrahymena vorax*, the plasmodium alternates between two forms: microstome and macrostome. The microstome feeds on bacteria. Depletion of the bacterial population can stimulate the microstome to differentiate into a macrostome which begins ingesting other ciliates or even its siblings. The presence of appropriate bacteria population stimulates the macrostome to dedifferentiate back to the microstome. In a cyst, the plasmodium can undergo progressive division yielding several offspring cells called tomites.

In Karyorelictea, the plasmodium contains two to many macronuclei.

In any genera (*Oxytricha*, *Euplotes*, *Blepharisma*, etc.), two plasmodia may become united by their dorsal regions forming the so called doublet. It is usually interpreted as the result of an abortive transverse fission, since the doublet undergoes a series of transformations necessary for return to the normal singlets. However, the doublets appear repeatedly and the successive series of their transformations is always the same, suggesting that the doublet stage is not simply an error of nature but rather an adaptation. In contrast to creeping singlets, the doublets of *Oxytricha bifaria* can swim and search for possible new spaces to colonize (Banchetti R and Erra F 2003).

In some genera, zygote produces a stalked sessile plasmodium. By conjugation, one partner is usually resorbed by other. In any few genera such as *Carchesium*, *Zoothamnium* (Song W *et al* 2002), the zygote produces a stalked plasmodium which gives rise to a branched colony of plasmodia with a common contractile stalk. In this sessile colony, plasmodia are small microzooids some of them can however differentiate into a large macrozooids which are then released to form new colonies. The number of plasmodia in the colony may be over 100. Zygotes can be produced both by autogamy and conjugation.

In genus *Stephanopogon*, the plasmodium contains 2-16 nuclei. However, it is unclear whether *Stephanopogon* belongs to Ciliophora (Corlis JO 1990b).

Bikonta: Corticata: (Alveolata): Dinoflagellata

Traditionally, Dinoflagellata are treated as a single-celled (Raven PH *et al* 1999, Taylor FJR 1990, Van den Hoek C *et al* 1995). But what is thought to be a single cell contains up to 100 typical DNA amounts and may be actually a plasmodium with unique "multinucleate" dinokaryon. In dinokaryon, the chromatin is permanently condensed during all stages of plasmodium life history. If the dinokaryon divides, its envelope remains intact during all stages of division and the entirely extranuclear spindle apparatus must pass through tunnels in envelope to attach chromosomes. After dinokaryon division is complete, the plasmodium immediately undergoes cytokinesis yielding two schizonts.

The zygote is a digenomic plasmodium with a chimerical dinokaryon. It may be either biflagellate and motile or non-flagellated and non-motile. The non-motile zygote is thick-walled, remains dormant during winter, and undergoes meiosis first during germination. Meiosis products are monogenomic plasmodia which then propagate producing many schizonts. At an unknown trigger, schizonts may become gametes which pair and fuse to form new zygotes.

In genus *Pheopolykrikos* of order Gymnodiniales, the schizont grows to a plasmodium bearing many dinokarya and several sets of flagella and flagellar furrows. This large plasmodium then fragments into dinospores each of which contains only one dinokaryon.

In genus *Gloeodinium* of order Phytodiniales, the non-motile schizonts are united into colony by thick, stratified sheaths of mucilage.

In few genera such as *Dinoclonium*, *Dinothrix*, and *Haplozoon*, schizonts remain in a filamentous colony, if they do not separate after dividing. The colony can even branch.

Bikonta: Corticata: (Chromista): Actinophryida

In genus *Actinosphaerium* (Febvre-Chevalier C 1990, Mikrjukov KA and Patterson DJ 2001), the zygote progressively propagates without cytokinesis until it becomes a spherical multinucleate plasmodium with numerous slender retractile pseudopodia

arranged radially. Soon or later, the plasmodium retracts all pseudopodia and releases a gelatinous envelope. After some nuclei disappear, the plasmodium undergoes cytokinesis to form a number of digenomic cells. Within the envelope, each digenomic cell becomes surrounded by separate cell wall and divides one time so that each cyst contains two digenomic cells. Each digenomic cell undergoes meiosis during which all but one monogenomic nucleus degenerate and the cell becomes a gamete. Within each cyst, both gametes fuse to form a new zygote.

In genus *Actinophrys*, the zygote sometimes gives rise to a sphaera-like cell association which however disintegrates later. Dispersed in environment, free living cells frequently alternate between various cell body forms accompanied by dramatic change in behavior so that these forms have been for a long time treated as a tens of different species scattered within a dozen of distinct genera. Some of these cell body forms are actually multinucleate plasmodia producing resting spores. Soon or later, the free living cell settles and encysts. Within the cyst, the binary fission produces two cells which undergo meiosis. After each meiotic division, one offspring nucleus degenerates so that the cyst contains only two tetrads. One tetrad differentiates into male gamete with pseudopodia oriented towards the other tetrad which becomes a female gamete. Fertilization results in an encysted zygote (Febvre-Chevalier C 1990).

Bikonta: Corticata: (Chromista): Bacillariophyta

In genus *Stephanopyxis* (Van den Hoek C *et al* 1995), the zygote gives rise to the cell colony. As soon as the cell colony consists of 8, 16, or 32 cells, it breaks. The division type is unique: one daughter cell is the same size as the mother cell while the other is smaller. It is shorter and narrower by about twice the thickness of the girdle. Thus, the average cell size decreases with each successive round of cell division. When the cells have decreased in size to between 0.4 and 0.2 of their original, maximum diameter, they become meiocytes and will undergo meiosis to form gametes if environmental conditions are suitable. Some cells, however, continue to divide until their progeny cells become too small and die. Smaller meiocytes usually produce male gametes, and larger meiocytes usually produce female gametes. The zygote swells and its expansion is accompanied by a concomitant growth of the zygote wall. At this stage, the zygote is called an auxospore. After karyokinesis, one of the daughter nuclei degenerate, the other moves across to the other side of the auxospore and performs a second karyokinesis, after which the new initial fristule is formed.

In some genera such as *Chaetoceros*, *Melosira*, *Rhizosolenia*, *Skeletonema*, etc., the usual primary body plan is a hypha of indefinite length (Round FE and Crawford RM 1990). There is however no evidence of cell interaction in hypha. Cells remain equivalent to each other and each cell can give rise to new hypha.

In genus *Licmophora*, for example, bilateral-symmetric cells form branching primary cell colony (Raven PH *et al* 1999, Round FE and Crawford RM 1990).

Cell aggregates which are formed when Bacillariophyta bloom are a primary source of marine snow (Thornton DCO 2002).

Bikonta: Corticata: (Chromista): Bicosoecida

Bicosoecida are poorly studied and little is known about their life history. But some of them are known that cells live in loose association (Dyer BD 1990a).

Bikonta: Corticata: (Chromista): Centroheliozoa

In genus *Raphidiophrys*, cells are often held together by cytoplasmic processes. Each cell has a thick gelatinous coat with minute spines.

Bikonta: Corticata: (Chromista): Chrysophyta

In variety of genera (Kristiansen J 1990, Raven PH *et al* 1999, Van den Hoek C *et al* 1995), cell associations occur during the life history of individual cell progression.

In genus *Hydrurus*, cells are loosely arranged in a gelatinous matrix. The hypha-like primary cell colony with apical growth may be up to 30 cm long. By branching and fragmentation of hyphae or by formation of flagellated spores, hyphae of the same individual cell progression become dispersed in environment.

In genus *Cyclonexis*, wheel-like primary cell colony is composed of 10 to 20 wedge-shaped cells. Young cell colony is funnel-shaped.

Genus *Dinobryon* is known for bush-like colonies of hyphae. The zygote forms typical cyst. Tetrad propagates forming a colony. In colony, each cell is surrounded by a vase-shaped case, a lorica, drawn out at its base. The lorica may be hyaline or cellulose. The elongated cell body is attached to the base of the lorica with its attenuated posterior tip. In colony, daughter cells remain attached to the inner margin of aperture of parent loricae and there secrete new loricae. Each cell can become a spherical cyst. Male and female colonies are similar. Also gametes are similar.

In genera *Monas* and *Ochromonas*, sphaera contains 20 to 50 biflagellate cells.

In genus *Uroglena*, sphaera is composed of ovoid cells arranged on periphery of a gelatinous mass. In sphaera, cells may be connected with one another by gelatinous processes running inward and meeting at a point. The sphaera divides by bipartition. Cysts are spherical.

In genus *Chrysocapsa*, primary cell colony is a sphaera. Within sphaera, cells are distributed rather without order. They are embedded in a mucilage envelope.

In genus *Chrysosphaera*, the sphaera is regular.

In genus *Synura*, the zygote forms a cyst enclosed in a siliceous wall. The germination of the cyst is accompanied by meiosis. Flagellate tetrads propagate and each forms a spherical or ellipsoidal colony. In this sphaera, ovoid cells held together by a gelatinous matrix are arranged radially. The sphaera is covered by tile-shaped siliceous scales having minute spines. Each cell can become a spherical cyst. The sphaera can also



fragment. Sphaerae of the same individual cell progression are dispersed in space. Male and female sphaerae are similar. Male gametes swim to female sphaerae and fertilize eggs.

Genus *Anthophysa* form colonies of sphaerae. In this secondary cell colony, sphaerae occur at tips of bush-shaped gelatinous matrix.

Bikonta: Corticata: (Chromista): Cryptophyta

Cryptophyta are usually motile biflagellate cells which continue to swim even during the division. In some species, however, non-motile cells tend to form colonies invested in multiple mucilaginous sheaths (Gillott M 1990).

Bikonta: Corticata: (Chromista): Dictyochophyta

In genus *Ciliophrys* (Febvre-Chevalier C 1990), cell propagation results in a rather irregular cell association containing sometimes over 100 cells. Cells are first spherical with extremely fine radiating pseudopodia, but some cells can become flagellated and swim away. Two or more cells often fuse together to form a multinucleate plasmodium. Also the plasmodium can produce one or more flagellated cells which are capable of pulling the whole mass slowly as they swim.

Bikonta: Corticata: (Chromista): Haptophyta

In genus *Pleurochrysis* (Green JC *et al* 1990, Van den Hoek C *et al* 1995), the zygotic cell progression is dispersed in space, but tetradic cell progressions consists of branching hyphae which clone themselves by production of zooids. Some zooids can become gametes.

In genus *Isochrysis* (Green JC *et al* 1990, Van den Hoek C *et al* 1995), young cells are non-motile, hemispherical, and form cuboidal masses. Older cells are spherical and surrounded by concentric layers of mucilage. Sometimes, the mucilage is secreted only on one side. In this case, a branched stalk can be built up, consisting of curved transverse layers. For a long period, this type of cell colony has been even treated as a separate species named *Chrysotila*.

In some Haptophyta (Green JC *et al* 1990, Raven PH *et al* 1999, Van den Hoek C *et al* 1995), there is a bloom-forming stage. In genus *Phaeocystis*, for example, it develops in mid-April or in May in the North Sea. The cells first form small spherical colonies. In the sphaera, cells are held together by a gelatinous matrix. Each initial primary sphaera gives rise to large lobed secondary colony. Numerous secondary colonies aggregate forming massive blooms. Storms often whip blooms into soapy foams.

Bikonta: Corticata: (Chromista): Hyphochytriomyceta

In Hyphochytriomyceta (Fuller MS 1990), when the flagellate cell stops swimming, it rounds and encysts. In genus *Rhizidiomyces*, the spore germination followed by progressive nucleus propagation results in development of a growing spherical

plasmodium with rhizoids. In genus *Hyphochytrium*, the spore germination includes emergence of the germ tube. The nucleus moves to the tip of the tube and propagates progressively. Concomitant with an increasing diameter of the germ tube, a swollen area develops. Tubes extend from the swollen area. Nuclei move into these tubes followed by a swelling of their tips. Thus, the polycentric habit of the hyphae colony is established and maintained.

Bikonta: Corticata: (Chromista): Labyrinthulida

Traditionally, Labyrinthulida have been grouped with the slime molds, but are now recognized to be distinct from them. It has also been discovered that they have an organelle, a bothrosome, that is capable of secreting ectoplasm outside their cells (Porter D 1990). Ectoplasm projections expand to form a network over which the cell can travel. The Labyrinthulida appear to be unique in this ability. The ectoplasmic network absorbs nutrients and attaches the cell to surfaces.

In genus *Labyrinthula*, spindle-shaped trophic cell progressively propagates producing cells that form colony which can increase indefinitely within the common ectoplasmic network. Cells exhibit gliding motility within the network. Enlarged cells undergo meiosis and release biflagellate zoospores.

In genus *Labyrinthuloides*, trophic cell progressively propagates to produce cells that separate from each other or may be held together within the parent wall to form a spherical colony, a sorus. The ectoplasmic network does not surround the developing sorus, but emanates from the basal side. Within the sorus, spores are produced and, when released, move apart by gliding on their individual ectoplasmic networks.

In genus *Thraustochytrium*, trophic cell grows by enlargement and progressive nuclear division to spherical multinucleate plasmodium. Progressive cleavage of the plasmodium produces spores which are released by dissolution of plasmodium wall. The spores develop into biflagellate zoospores.

In genus *Schizochytrium*, trophic cell divides by two successive divisions to form cluster of four cells. Each cell propagates producing a sorus releasing several biflagellate zoospores.

Bikonta: Corticata: (Chromista): Oomyceta

In most Oomyceta (Dick MW 1990, Raven PH *et al* 1999), large colonies of hyphae are formed during the life history of individual cell progression. For example, in genus *Saprolegnia*, the zygotes become free first after long period of dormancy. Each free zygote germinates and progressively propagates forming a short hypha with a tube-like spore case, a sporangium, at the tip. Released spores are free-swimming biflagellate cells which first migrate before they encyst. If time is ripe, the spore germinates and propagates building a hypha that increasingly branches forming a large bush-like colony of hyphae. Hyphae release cellulose wall. In the colony, sporangia are built at tips of hyphae and release numerous spores for further distribution of the individual cell progression in space. Secondary cell colonies of different individual cell progressions

usually superpose each other. At some hyphae, specialized sporangia, oogonia and antheridia, are built. In oogonia, cells undergo meiosis and tetrads immediately differentiate into large eggs. In antheridia, cells undergo meiosis without cytokinesis and become plasmodia each with four monogenomic nuclei. Coming together with an oogonium, the antheridium forms tubes through which monogenomic nuclei can enter oogonium and fertilize eggs. Newly formed zygotes become thick-walled oospores.

Bikonta: Corticata: (Chromista): Opalinida

Opalinida are symbionts in the posterior end of digestive tract of vertebrate hosts (Corlis JO 1990a). In genus *Opalina*, the zygote encysts and leaves the host gut with feces. The new host is usually a tadpole approaching a metamorphosis. In the new host, the zygocyst gives rise to a rounded multinucleate plasmodium with many rows of cilia. This feeding stage, a trophont, grows to large flattened plasmodium with flexible, leaf-like body which often exhibits a shape resembling a scalene triangle. In response to changes in host preceding its breeding season, the plasmodium begins a series of divisions without intervening growth, a palintomy. Small plasmodia transform into infective cysts which leaves the host gut to be ingested by newly hatched tadpoles. In their guts, plasmodia excyst and undergo division with meiosis producing micro- and macrogametes bearing many flagella. The gametes fuse, the digenomic zygotes round up and transform into zygocysts.

Bikonta: Corticata: (Chromista): Pelagophyta

In genus *Chrysonephos* (Boddy S *et al* 1999), the cell association occurs in form of a hypha provided with an external wall consisting of microfibrills. Hyphae are embedded in a mucilaginous envelope which favors their aggregation. Inside the hypha, the cells may differentiate into flagellate zoospores.

Bikonta: Corticata: (Chromista): Phaeophyta

Phaeophyta dwell almost exclusively in marine or coastal environment. There are only a few rare freshwater brown algae.

Most individual cell progression species of Phaeophyta form large colonies of hyphae (Clayton MN 1990, Raven PH *et al* 1999, Van den Hoek C *et al* 1995). The complexity of the colonies varies enormously from macroscopic branched hyphae to foliose plants many meters long.

In genus *Laminaria*, for example, the zygote propagates forming a multicellular sporophyte. The sporophyte body develops from an initial hypha to a massive three-dimensional colony of tightly connected hyphae, a kelp. The kelp is covered by a gelatinous sheath and consists of a root-like holdfast attached to the firm substrate, a stem-like stalk, a stipe, and numerous leaf-like blades branching from the stipe. In kelp, cellular connections occur not only between cells of a particular hypha but also between cells of neighboring hyphae. In cortical regions, hyphae fuse and filamentous organization of the secondary cell colony is not more evident. Hyphae also show signs of differentiation. At the surface of the kelp, some hyphae develop into sporangia where

cells undergo meiosis. Tetrads differentiate into zoospores, free-swimming biflagellate cells. After a period of migration, each zoospore gives rise to a multicellular gametophyte which develops from an initial hypha to a small bush-like colony of hyphae. Although all zoospores look similar, the gametophyte becomes either a female or a male. In gametophyte, cells at the tips of hyphae differentiate into gametes. Female gametophyte produces large eggs, male gametophyte - free-swimming sperm. If sperm fertilize eggs and zygotes propagate, new sporophytes overgrowth the maternal gametophyte.

In some genera, sporophyte and gametophyte are quite similar in appearance to each other. But mostly, the sporophyte is much larger as the gametophyte.

Genus *Fucus* has no free-living gametophyte at all. The zygote is floating. Upon landing in an acceptable habitat, zygote will develop into kelp which tips often contain gas bladders and conceptacles which have either oogonia or antheridia producing eggs and sperm respectively.

In some genera, kelps are especially huge. For example, in genera *Nereocystis* or *Macrocystis*, kelp is of about 50-100 m long and grows in deeper water anchored to the bottom by their holdfasts. Kelps of genus *Sargassum* sometimes break off from their holdfasts and form floating masses. They stay afloat by producing gas-filled bladders which act like buoys.

Bikonta: Corticata: (Chromista): Xanthophyta

In Xanthophyta (Van den Hoek C *et al* 1995), formation of cell associations during life history of individual cell progressions is abundant.

In order Tribonematales, cells form a long hypha. Cell body is cylindrical or fusiform swelled at the center. Cell wall consists of two parts overlapping at the midregion. Individual cell progression grows either by fragmentation of hyphae or by production of some kind of spores. Spores may be flagellated and free-swimming zoospores, or they may be non-flagellated aplanospores.

In order Vaucheriales (Gavrilova OV and Rudanova EE 1999, Gavrilova OV *et al* 2000), the zygote forms a cyst with a thick wall and becomes a hypnozygote. After germination, the zygote produces a tubular hypha which is a multinucleate plasmodium with no internal partitioning into cells. Hyphae branch irregularly. The hypha clone itself by fragmentation or by either aplanospores or zoospores. Round aplanospores are formed at the tip of sporangium. After maturation, a deep green aplanospore, which demonstrates dense packing of nuclei and chloroplasts, is released from the sporangium. The amount of nuclei in mature aplanospore is about 2000. All nuclei are involved in the process of karyokinesis. All nuclei divide simultaneously. Individual mitotic stages coincide in time. Mitotic spindle is completely closed. Nuclear envelope remains intact until the late telophase. The germination of aplanospore occurs without a lag period immediately after release from the sporangium. The duration of germination time varies. At the end of germination, all nuclei and chloroplasts migrate from the aplanospore towards the vegetative branch. Vegetative thallome is formed as a result of

the aplanospore germination. Thallome consists of the branching tubular filaments with no septae. The thallome exhibits tip, or apical, growth. A site of expansion in tip-growing cells is associated with dome-shaped apex of the filament, which results in characteristic tubular morphology. Apical growth is characterized by the highly determined localization and movement of organelles, as well as by polarization of the synthesis and secretion of cell wall precursors. Meiosis takes place immediately before the formation of gametes. Each antheridium produces numerous spermatozooids. On the contrary, the ripe oogonium contains only one single egg ready for fertilization.

In order Botrydiales, the multinucleate plasmodium is usually a sphaera with numerous branching extensions which function as rhizoids to anchor in soil. The plasmodium can divide up into a large number of zooids, which are liberated from the plasmodium when the environment is flooded with water. If the plasmodium begins to dry, it retracts into the rhizoids and form thick-walled resting spores. The spore germinates with production of zooid.

In order Mischococcales, elongate cylindrical plasmodia are often bent and are attached by a short stalk (for example, genus *Ophiocyttium*). The uppermost part of the plasmodium wall opens like a lid to liberate the spores. The emerging spores often settle on the rim of the parent plasmodium wall and there grow up into new plasmodia.

Bikonta: Corticata: (Plantae): Glaucophyta

Glaucophyta are rare in nature (Kies L and Kremer BP 1990). In some species, cells tend to form colonies (for example, *Gloeochaete wittrockiana*). In other species, karyokinesis produces multinucleate plasmodium which divides by infurrowing of the plasma membrane (for example, *Glaucocystis nostochinearum*).

Bikonta: Corticata: (Plantae): Rhodophyta

In Rhodophyta (Gabrielson PW *et al* 1990, Raven PH *et al* 1999, Van den Hoek C *et al* 1995), formation of cell associations during life history of individual cell progressions is abundant.

Class Bangiophyceae

In order Porphyridiales, individual cells are embedded in a common mass of mucilage forming either a spherical (genus *Porphyridium*) or filamentous (genus *Chroodactylon*) colony. Gametes and zygote are unknown.

In genus *Erythrotrichia* of order Erythropeltiales, the zygote grows into an upright, unbranched filamentous cell colony, a sporophyte, which is anchored to the substratum by short rhizoids. The upper cell acts as a spore which escapes the colony and then gives rise directly to a new colony, thus effecting the distribution of individual cell progression in space. Mature sporophyte produces meiospores. Each meiospore grows into tiny filamentous gametophyte with three cells. The apical cell of this dwarf gametophyte swells, cuts off a male gamete, and become an oogonium. In other Erythropeltiales, the cell colony is either a tiny blade or a disc.

In the only known species of order Rhodochaetales, *Rhodochaete parvula*, the zygote develops into single digenomic carpospore which is released from the maternal gametophyte and gives rise to a digenomic multicellular sporophyte. The sporophyte grows as a branched colony of hyphae. Young sporophyte can clone itself by production of digenomic spores. Mature sporophyte develops meiosporangia within which monogenomic meiospores are produced. Each meiospore grows into a multicellular gametophyte which looks alike the sporophyte. In mature gametophyte, the female gametangium is almost indistinguishable from surrounding cells and differentiates into egg. Tiny male gametangia are cut off from other cells by curved lateral walls and produces male gametes. They however are not flagellated and, if released from the gametophyte, are rather carried by water currents to find and fertilize eggs.

In genus *Porphyra* of order Bangiales, the zygote propagates within the maternal oogonium producing a number of 4, 8, 16, or 32 digenomic carpospores. At this stage, the maternal oogonium is called a carpogonium. Carpospores are usually released by the breaking of the carpogonium wall. Each carpospore gives rise to a branched colony of hyphae, a sporophyte, which for a long period of time has been treated as a separate genus *Conchocelis*. The sporophyte produces a special type of sporangia, a conchosporangia, within which the cells differentiate into digenomic conchospores. During conchospore germination, meiosis takes place and tetrads become arranged in a row in the four-celled, uniseriate germling which subsequently gives rise to single multicellular leaf-like gametophyte. The leaf is almost always one cell thick. It is irregularly folded. Its base is anchored to the substratum by rhizoids. Young gametophyte can clone itself by production of spores along the upper margin of the sheet. Mature gametophyte usually develops both male and female gametangia, but some completely male gametophytes do occur. The female gametangium resembles surrounding cells and differentiates into an egg. The spermatangium, on the contrary, changes producing a new wall layer and progressively propagates producing up to 128 tiny male gametes. They however are not flagellated and, if released from the male gametophyte, are rather carried by water currents to find and fertilize eggs. After fertilization, zygotes are still retained on the maternal gametophyte and develop into the carpogonia.

#### Class Florideophyceae

Generally, the zygote propagates producing a multicellular carposporophyte which develops from an initial hypha to the bush-like colony of hyphae. The carposporophyte produces carpospores, releases them and die. After germination, each carpospore develops into a multicellular tetrasporophyte which produces tetrasporangia where cells undergo meiosis with subsequent differentiation of tetrads into tetraspores. Each tetraspore develops into a multicellular gametophyte of either female or male types. Both the tetrasporophyte and gametophyte can clone itself by digenomic and monogenomic spores respectively. Female gametophyte produces carpogonia with eggs that are retained on the gametophyte. Sperm are not flagellated and, if released from the male gametophyte, are rather carried by water currents to find and fertilize eggs. After fertilization, zygotes are still retained on the maternal gametophyte and develop into the carposporophytes.

In some Rhodophyta, cell associations are coralline, secreting a hard shell of calcium carbonate crystals around themselves.

Bikonta: Corticata: (Plantae): Viridiplantae

Phylum Chlorophyta (green algae)

Class Chlorophyceae

Numerous individual cell progression species of Chlorophyceae are characterized by association of the cells (Melkonian M 1990, Raven PH *et al* 1999, Van den Hoek C *et al* 1995). However, the zygote does not propagate but often serves as a resting spore which remains dormant during a period of potentially damaging environmental changes such as desiccation. After germination, it immediately undergoes meiosis. Each tetrad then produces cell association by progressive propagation. There is a wide variety of shapes and forms of cell associations, including hyphae and sphaerae.

In order Oedogoniales (Raven PH *et al* 1999, Van den Hoek C *et al* 1995), the zygote undergoes meiosis which is preceded by a period of dormancy. The meiosis produces four meiospores. Two meiospores give rise to relatively broad female hyphae, the other two to thinner male hyphae. Hyphae clone themselves by production of zoospores. The zoospore swims around before attaching itself to the substratum and growing into a new hypha. Female hypha can form large swollen cells which give rise to oogonium mother cell, while the male hypha produces small discoid sporangia arranged in stacks. Each male sporangium forms a male spore which become released, swims and, if attracted to any female hypha, attaches itself to it. The same female hypha attracts many male spores which then stimulate the oogonium mother cells to develop oogonia. Then, each male spore develops into dwarf antheridium which produces two flagellate male gametes. The newly formed zygotes remain enclosed within the oogonia for a long time.

In order Chlorosarcinales (Van den Hoek C *et al* 1995), the colony is a more or less cubical group or packet of cells.

Order Sphaeropleales

In order Sphaeropleales (Van den Hoek C *et al* 1995), the zygote becomes a hypnozygote which then gives rise to a filamentous colony consisting of elongate, cylindrical multinucleate hyphae. Each hypha contains a number of ring-like accumulations of cytoplasm separated by large vacuoles. Each ring harbors several nuclei. The colony can fragment by dissociation of hyphae. Gametes are produced within the hyphae. The hypha produces either a many small biflagellate male gametes or a smaller number of eggs. Fertilization and hypnozygote formation occur within the female hypha.

In genus *Hydrodictyon* (Raven PH *et al* 1999, Van den Hoek C *et al* 1995), the zygote develops into a spherical resting stage, the hypnozygote. After a period of dormancy, the hypnozygote germinates, undergoes meiosis, and releases four biflagellate

zoospores. Each zoospore forms an irregularly shaped multinucleate plasmodium bearing pointed projections. This stage is called a polyeder. The contents of the polyeder divide up into zooids which are then discharged into a vesicle. When the vesicle is extruded from the polyeder, the zooids order themselves into a more or less spherical net-like colony. Within this initial colony, each cell in turn becomes a multinucleate cylindrical plasmodium which may contain up to 20000 small biflagellate zooids. The zooids exhibit only a few transient, convulsive movements and soon become associated laterally to produce a young daughter net-like colony which is then liberated through the disintegration and dispersion of the mother plasmodium wall and matures to the large colony of cylindrical plasmodia. The zooid can also be liberated individually. In this case, it swims around freely, then comes to rest, loses its flagella, and transforms into hypnospor. The germination of hypnospor results in the zoospore which then gives rise to the polyeder and so on. Soon or late, the formation of biflagellate gametes is triggered which immediately undergo syngamy to form new zygotes.

In genus *Pediastrum* (Van den Hoek C *et al* 1995), the zygote gives rise to hypnozygote from which zoospores emerge on germination. Each zoospore gives rise to the polyeder which in turn produces the initial colony. This colony is circular, flat and radially organized. It is usually one cell thick. The cells around the colony margin bear horn-like projections. Each of these cells becomes a multinucleate plasmodium which produces biflagellate zooids. These are always discharged together into a vesicle which is then extruded from the mother plasmodium.

In order Chaetophorales (Raven PH *et al* 1999, Van den Hoek C *et al* 1995), elongated, cylindrical cells form a hypha (for example, genus *Uronema*). Primary hypha can give rise to a branched (for example, genera *Stigeoclonium*, *Draparnaldia*) or solid (for example, genus *Schizomeris*) colony of hyphae. Each cell can produce a quadriflagellate zoospore.

#### Order Chlamidomonadales

In family Volvocaceae (Desnitski AG 2000, Kirk DL 2003, Kirk DL and Nishii I 2001, Nozaki H and Krienitz L 2001), usual form of the cell associations in tetradic cell progression is a sphaera (Raven PH *et al* 1999, Van den Hoek C *et al* 1995). In sphaera, cells are connected by fine cytoplasmic bridges, plasmodesmata, which may be important in coordinating the development and behavior of the cell association. Sphaerae are usually of precise geometric shape.

In genus *Gonium*, for example, the cell association is a concave sphaera made of 4 to 32 cells. Their flagella beat independently, but since they are all oriented in the same direction, they are able to propel the sphaera through the water. However, cells remain equivalent to each other. In genus *Pandorina*, the sphaera consists of 8, 16, or 32 cells attaching closely to each other in a gelatinous matrix. The sphaera of genus *Eudorina* contains 16 to 32 cells, of genus *Pleodorina* - 64 to 128 cells.

Most elaborated is the sphaera of genus *Volvox*. The cells live in temporally shallow ponds that fill with spring rains but dry out in the heart of the summer. Just shortly



before the pond dries up, zygotes are produced. For a long time, they remain however dormant to survive the heat and drought of late summer and the cold of winter. When rain fills the pond in spring, each zygote breaks dormancy and immediately undergoes meiosis. Each tetrad progressively propagates, whereas cells remain associated in a hollow sphaera. In sphaera, the cells are connected by plasmodesmata and are also imprisoned in a rigid honeycomb of chambers walled with cellulose. Within the sphaera, there is some division of labor among cells. Most cells are small and biflagellate. The beating of flagella is coordinated to propel the body along like a rolling ball. Any few cells differentiate into large gonidia which are usually confined to one end of the sphaera, where they give rise to new miniature sphaerae. New sphaerae are initially sheltered inside the large parent, while their cells are oriented with flagella interiorly and they must therefore turn themselves right side out. If this is done, they are released from the parent sphaera and swim away. Thereafter, the cells of parent sphaera commit suicide, whereas juvenile sphaerae grow, mature, and produce the next generation of juvenile sphaerae. This event repeats many times until the pond is about to dry up. Gonidia undergo modified pattern of specialization and differentiate into eggs or sperm. The sperm are to be released and swim up to non-motile eggs. After fertilization, large number of new zygotes is produced. Thus, a particular individual cell progression lives only one year.

Interestingly, in genus *Chlamidomonas* (Van den Hoek C *et al* 1995), the sphaera is formed only if free-living monogenomic cells become gametes and are ready for syngamy. When these cells are brought together, a very characteristic phenomenon occurs, a clumping. The gametes unite into groups very quickly. Each clump begins with association of two cells of different mating types via their flagella. Other gametes also attach themselves to this pair producing a clump.

#### Class Ulvophyceae

In Ulvophyceae (Floyd GL and O'Kelly CJ 1990, Raven PH *et al* 1999, Van den Hoek C *et al* 1995), the zygote usually propagate forming a sporophyte.

In order Dasycladales (Floyd GL and O'Kelly CJ 1990, Raven PH *et al* 1999, Van den Hoek C *et al* 1995), the zygote germinates immediately and grows into the uninucleate plasmodium. For instance, in genus *Acetabularia* (Dumais J *et al* 2000, Mandoli DF 1998), the plasmodium consists of three parts: a root-like rhizoid, a tiny stalk, and a flattened umbrella-like cap. In young sporophyte, the nucleus resides within the rhizoid and expands enormously developing into the giant nucleus. In mature sporophyte, the giant nucleus gradually decreases in size and undergoes meiosis. Subsequent rounds of karyokinesis lead to production of up to 20000 tiny nuclei which are transported to the cap by cytoplasmic streaming and become concentrated in the rays, gametangia. Cleavage of the gametangia produces cysts, each with a single monogenomic nucleus. The contents of the sporophyte are almost wholly used up during formation of cysts so that it subsequently disappears. The cyst usually requires a period of dormancy before it germinates. In the meantime, it becomes a multinucleate plasmodium. Upon germination, the cyst content divides up into numerous biflagellate gametes which then become set free through an opening in the cyst wall.

In order Cladophorales (Floyd GL and O'Kelly CJ 1990, Raven PH *et al* 1999, Shepherd VA *et al* 2004, Van den Hoek C *et al* 1995), the sporophyte is first a multinucleate plasmodium which then gives rise to a bush-like colony of plasmodia. In mature sporophyte, each plasmodium can swell somewhat and its content divides into monogenomic quadriflagellate meiospores which then exit through a pore at the upper end of the plasmodium. Each meiospore develops into gametophyte. Sporophyte and gametophyte look alike and can be distinguished only by the size of the cell or by nucleus. Also their development follows essentially identical pathways. Gametophytes produce biflagellate gametes of both mating types which are similar to each other in appearance.

In order Caulercales (Van den Hoek C *et al* 1995), the zygote attaches itself to the substratum and grows slowly into a tiny branched plasmodium which initially contains one single enormous nucleus. This nucleus then divides many times to give a large number of small nuclei. The plasmodium subsequently can cleave up into multiflagellate, multinucleate zoospores. Probably, the meiosis takes place during this process, since about half of the zoospores grow into male gametophytes and half into female gametophytes. The sporophyte may itself bud off gametophytes directly. Gametophytes are also plasmodia. They can have a bubble-like (for example, genus *Derbesia*), bush-like (for example, genus *Bryopsis*), or leaf-like (for example, genus *Caulerpa*) appearance. Mature gametophytes develop gametangia producing biflagellate gametes. Male and female gametes look differently.

In order Ulotrichales (Van den Hoek C *et al* 1995), the quadriflagellate zygote swims down, attaches itself to the substratum, and becomes immobile. It germinates only short-day conditions, when it swells up into the large stalked cell. Its contents divide up to give 4-16 quadriflagellate zoospores. During this process, the meiosis probably occurs. Each zoospore swims down, attaches itself to the substratum, and gives rise to an unbranched hypha. All cells in the hypha are able to divide. The hypha clone itself by production of quadriflagellate zoospores. From 2 to 16 zoospores are produced per cell. They are initially discharged into the vesicle and then released from the parent cell. In long days, the hyphae produce biflagellate gametes which are smaller than the zoospores. The same hypha produces gametes of the same mating type. Gametes fuse to form quadriflagellate zygotes.

In order Acrosiphoniales (Van den Hoek C *et al* 1995), the zygote develops into the large stalked cell within which the meiosis occurs and quadriflagellate zoospores are produced. Each zoospore gives rise to the multinucleate hypha which then produces either unbranched (for example, order *Urospora*) or branched (for example, genus *Acrosiphonia*) hyphae colony attached to the substratum by several rhizoids. Each hypha can divide its content into many quadriflagellate zoospores each of which gives rise to new colony of multinucleate hyphae. Male hyphae produce male gametes which are smaller than female gametes produced by female hyphae. Gametes are biflagellate.

#### Order Ulvales

In genus *Monostroma* (Van den Hoek C *et al* 1995), the zygote develops into the large stalked cell which then bores into the calcareous shell of cirripeds and takes on an

irregular outline with a number of protrusions. In this condition, it spends a summer. Germination of the zygote produces quadriflagellate zoospores which are released through a discharge tube. Each meiospore attaches itself to the substratum and grows to form first a discoid and then a hollow spherical cell colony. This colony ruptures at its upper end and becomes sac-shaped. The sac splits and gives rise to a leaf-like gametophyte, only one layer of cells thick. The leaf grows up to 20 cm high and is irregularly undulate and folded. The female gametophyte produces rather larger gametes than the male gametophyte. In both cases, gametes are biflagellate.

In genus *Ulva* (Dion P *et al* 1998, Malta EJ *et al* 1999, Raven PH *et al* 1999, Van den Hoek C *et al* 1995), the zygote germinates immediately and gives rise to the massive three-dimensional colony of tightly connected hyphae which is called a sea lettuce because of its leafy appearance. This leafy sporophyte is two cells thick but can be a meter long. It can be free-floating or attached to the substratum. Cells in the marginal part of the sporophyte undergo meiosis producing a numbers of quadriflagellate meiospores. Half of the meiospores grow into male gametophytes, while the other half grow into female gametophytes. Mating type determination occurs during meiosis. Gametophytes are similar to the sporophyte in development and appearance. Gametophyte produces biflagellate gametes of two types.

#### Class Trebouxiophyceae

In order Prasiolales (Van den Hoek C *et al* 1995), the zygote is first binucleate. It is uniflagellate and can swim around for some time. After a few days, a karyogamy occurs within the zygote which then comes to rest, germinates, and gives rise to a leaf-like colony of hyphae. The leaf is only one cell thick. The sporophyte clone itself by digenomic aplanospores. Regions of the sporophyte, where the formation of aplanospores occurs, become two- or four-layered. In mature sporophyte, meiosis takes place in the upper parts. Tetrads progressively propagate producing gametophytes which remain attached to the sporophyte. Half of the gametophytes are male, the other half is female. The mature gametophyte completely consists of gametes which generally become discharged together in large numbers, simultaneously. The male gametes are small motile biflagellate cells, while the female gametes are large and non-motile. If any male gametes touch egg, it becomes absorbed so that a uniflagellate, binucleate zygote is produced.

#### Phylum Streptophyta

##### Class Zygnemophyceae

In order Zygnematales (Graham LE *et al* 2000, Hoshaw RW *et al* 1990, Raven PH *et al* 1999, Van den Hoek C *et al* 1995), almost all individual cell progression species live in freshwater environment making up the filamentous periphyton growing on and around the larger aquatic plants. The zygote of genus *Spirogyra*, for example, is a resting spore which withstands winter and undergoes meiosis only in spring. Each tetrad produces a hypha which cells divide in one plane producing end-to-end chain of cells. The hypha can be anchored to objects in the water by a rhizoid cell. The hyphae usually fragment to distribute the tetradic cell progression in space. The gametes are non-motile. To

produce new zygote, two hyphae of different mating types line up beside one another aligning neighboring cells which then produce conjugation tubes. The cells from one hypha can move over into the other hypha or, alternatively, cells from both hyphae can move into the conjugation tube. In either case, the cells of two mating types meet and fuse together producing zygotes which then develops into resting spores.

In order Desmidiaceae (Hoshaw RW *et al* 1990, Raven PH *et al* 1999), only few individual cell progression species form cell associations. Like Zygnematales, their zygotes are resting spores, their tetradic cell progression grows as long hyphae, and their zygotes are produced by conjugation.

#### Class Chlorokybophyceae

In Chlorokybophyceae (Graham LE *et al* 2000, Van den Hoek C *et al* 1995), cells are grouped into more or less cubical packet and are embedded in a common gelatinous matrix. Many packets in turn form a large mucilaginous colony. Within the colony, biflagellate zoospores are formed.

#### Class Klebsormidiophyceae

In Klebsormidiophyceae (Graham LE *et al* 2000, Van den Hoek C *et al* 1995), cell propagation leads to formation of a non-branching hypha which dissociates easily into fragments containing one to a few cells. Each cell is able to transform into a biflagellate zoospore which can swim away and develop into a new hypha after settling. Formation of gametes and their fusion to zygote have not been documented.

#### Class Charophyceae

In order Charales (stoneworts and brittleworts) (Graham LE *et al* 2000, Raven PH *et al* 1999, Van den Hoek C *et al* 1995), the mature zygote sinks into the sediments and becomes dormant for a short or long period of time. During germination, meiosis takes place producing a quadrinucleate cell which then divides into a small outer uninucleate cell and a larger inner trinucleate cell. All three nuclei of the inner cell subsequently degenerate. The outer cell gives rise to a multicellular gametophyte which develops to a colony of hyphae. It consists of a series of so called "giant cells" up to several centimeters in length with branches coming off at nodes composed of smaller cells. The gametophyte is anchored in mud or silt by translucent rhizoid cell. Growth occurs at the apex. Oogonia and antheridia grow at the nodes. Oogonium is oblong and consists of a central cell surrounded by five tubular, spiraling cells. A crown of smaller cells sits atop these cells where they come together. Antheridium is spherical. Mature male gametes are biflagellate.

In order Coleochaetales (Graham LE *et al* 2000, Raven PH *et al* 1999, Van den Hoek C *et al* 1995), the zygote undergoes meiosis after a period of dormancy. Tetrads propagate to produce 8 to 32 cells which then become biflagellate zoospores. When released, the zoospores swim away and each begins life as a multicellular gametophyte. It is a tiny discoid or a cushion-like colony of hyphae. Gametophyte can produce free-swimming biflagellate zoospores which leave the parent colony to begin new colonies. Colonies

may be found in freshwater habitat either growing on larger aquatic plants or attached to rocks or soil. In each gametophyte, cells can differentiate either into a large non-motile egg in oogonia or into smaller free-swimming biflagellate sperm in antheridia. Each antheridium produces only one single sperm which becomes surrounded by other cells. Newly formed zygotes are usually retained on the maternal sporophyte. The surrounding cells propagate to produce a layer of sterile tissue which envelops the zygote and may provide nourishment until zoospores swim away.

#### Phylum Cormophyta (land plants)

Cormophyta are also called Embryophyta, since the young sporophyte begins its development within the tissue of its parent gametophyte.

In Marchantiophyta (liverworts) (Graham LE *et al* 2000, Raven PH *et al* 1999), the zygote develops into a multicellular sporophyte which is a massive three-dimensional colony of tightly connected hyphae. This colony is composed of foot, short stalk, and capsule. Monogenomic spores produced within the capsule are disseminated by wind. After germination, each spore develops into a multicellular gametophyte which is much larger than a sporophyte. It is flat and lobed. The three-dimensional growth is highly organized. Cell differentiation produces a variety of specialized cell types. The lower surface of the gametophyte bears numerous rhizoids, hair-like projections, which anchor it and absorb nutrients from the soil. On the smooth upper surface of the gametophyte, there are gemmae caps or archegonia and antheridia. Gemmae caps contain spores to distribute tetradic cell progression in space. Archegonia are umbrella-headed stalks where eggs are produced. Antheridia are disk-headed stalks where flagellated sperm are produced. Sperm swim to the vicinity of the eggs in a continuous film of water and fertilize those producing zygotes.

In Bryophyta (mosses) (Gilbert SF 2000, Raven PH *et al* 1999), the zygote progressively propagates producing a multicellular sporophyte which is a massive three-dimensional colony of tightly connected hyphae. The colony consists of a foot, a stalk, and a capsule. Meiosis within the capsule yields monogenomic spores of two distinct types: female or male. They are released and eventually germinate, each progressively propagating to form either female or male multicellular gametophyte. Also in Bryophyta, the gametophyte, rather than the sporophyte, is the more conspicuous. Development of a gametophyte begins with an initial hypha which first gives rise to a colony of hyphae, a protonema, anchored to soil by rhizoid. Three days of favorable growing conditions produce upright shoots covered with leafy structures. The development of the gametophyte illustrates the transition from a filamentous to a highly organized three-dimensional growth type. The gametophyte can fragment to distribute tetradic cell progression in space. The shoots bear archegonia or antheridia at their tips. Female gametophyte develops archegonia where any cells differentiate into eggs. Male gametophyte develops antheridia where any cells differentiate into flagellated sperm which however need external water to reach eggs. If chemically attracted to the entrance into an archegonium, sperm fertilize the eggs to produce new zygotes. The embryonic sporophyte develops within the archegonium, and the mature sporophyte stays attached to the mother gametophyte. At first, the sporophyte is green and photosynthetic. At

maturity, it is brown, not more photosynthetic, and is nourished by mother gametophyte.

In Pteridophyta (ferns) (Gilbert SF 2000, Raven PH *et al* 1999), the zygote progressively propagates producing a massive three-dimensional colony of tightly connected hyphae. Young sporophyte develops a root-bearing rhizome from which fronds project. Fronds are variable in size and shape. Nearly all fronds first appear as a fiddlehead which unrolls as it grows. Fronds are secondarily subdivided into leaflets. They may have evolved by uneven branching. The sporophyte ranges in size from low-growing moos-like forms to tall trees. Sporophyte develops vascular tissue to conduct water and minerals up from the soil and to transport organic nutrients from one part to another. Within sporangia located in sori on underside of leaflets, meiosis yields tetrads differentiating into spores. They are released and disperse mostly by wind. After germination, each spore progressively propagates to form a multicellular gametophyte which grows and develops both archegonia and antheridia. Flagellated sperm use water to swim from antheridia to archegonia and to fertilize eggs. The embryonic sporophyte develops within the archegonium, and the mature sporophyte stays attached to the mother gametophyte. It remains photosynthetic and soon outgrows the space.

In gymnosperm Spermatophyta (seed ferns, cycads, conifers and others) (Gilbert SF 2000, Raven PH *et al* 1999), the sporophyte develops roots, stem, and leaves. Roots anchor a sporophyte in soil and give support. Numerous root hairs absorb water and minerals from the soil. Stem forms main axis, along with lateral branches, produces leaves and arrays them to be exposed to as much sun light as possible. Leaves are adapted to maximize photosynthetic activity. Leaves that bear sporangia are called sporophylls. They are arranged on cones. The sporophyte produces cones of two types: female seed cones and male pollen cones. Each scale of a seed cone has two ovules surrounded by an integument and with one opening at one end. In sporangium within the ovule, the cell undergoes meiosis producing four tetrads which directly differentiate into female spores. One female spore develops into a multicellular female gametophyte with 2 to 6 archegonia, each containing a single large egg. Each scale of pollen cone has two or more sporangia on underside. Within the sporangium, each cell undergoes meiosis and produces four tetrads which immediately differentiate into male spores. Each male spore develops into an immature male gametophyte, a pollen grain, consisting of two or three cells. Thus, gametophytes are diminutive, reduced to a mere few cells. Pollen grains remain on the sporophyte for only a short time. They are released and carried by wind to female seed cones where they land and germinate. After germination, the pollen grain matures to produce male gametes and to develop a pollen tube that grows into the female gametophyte. Pollen tube growth is quite slow, up to a year. After fertilization, ovule matures and becomes a seed composed of embryo, reserve food, and coat. Seed cone opens to release seeds. Under appropriate conditions, seed germinates and produce young sporophyte.

In angiosperm Spermatophyta (flowering plants) (Gilbert SF 2000, Raven PH *et al* 1999), the sporophyte develops roots, stem, and leaves. Once the sporophyte becomes mature, it initiates the development of flowers. The flower contains highly modified leaves arranged in rings. The first ring becomes green sepals which enclose the flower before it opens. The second ring becomes large and colorful petals. Sepals and petals are

sterile. The third ring becomes a pollen-producing stamens. Stamen is a slender stalk with an anther at the tip. Anther is a modified sporophyll and contains male sporangia where cells undergo meiosis and tetrads differentiate into male spores. Each male spore develops into a mature male gametophyte, a pollen grain. The pollen grain contains of three cells two of which are sperm. The fourth ring of leaves within the flower becomes carpels which fuse to form a pistil. Carpel is a modified sporophyll and consists of the stigma, the style, and the ovary. The ovary contains one or more ovules attached by a placenta to the ovary wall. The ovule has one or two outer layers of cells, integuments, which enclose the female sporangium where the cell undergoes meiosis and tetrads differentiate into female spores. The largest of these spores undergoes three mitotic divisions to produce a female gametophyte which is a seven-celled embryo sac with eight nuclei. The cell with two nuclei is called a central cell. One of uninucleate cells is the egg. If released, pollen grains can be transferred to the carpels by various agencies such as wind, water, or animals. After any pollen grain lands on the stigma of the carpel, it takes up water and the pollen tube emerges. The pollen tube grows down, passes between cells of stigma and style, enters the ovule through opening and discharges both sperm. One sperm fertilizes the egg to produce zygote which propagates forming an embryo and a suspensor. The suspensor anchors embryo and transfers nutrients to it from the sporophyte. Another sperm unites with central cell to form digenomic triploid cell which gives rise to the endosperm (Berger F 2003, Olsen OA 2001). The endosperm develops into nutritive tissue. The ovule develops into seed, the ovary develops into a fruit. Different kinds of fruit employ different kinds of dispersal mechanisms for dissemination of seeds. Under favorable conditions, seed germinates to produce young sporophyte.

Unikonta: Opisthokonta: Fungi

Most Fungi form cell associations (Raven PH *et al* 1999). Typical form of the primary cell colony is a hypha which is actually a tube-shaped plasmodium enclosed by a rigid chitinous wall. Some hyphae have cross walls, septa, with pores which allow cytoplasm and organelles to pass freely. Fungal hyphae are microscopic, but the radially-expanding secondary cell colony, a mycelium, can be very large rivaling the mass of the largest plants and animals. Fungi are non-motile. They move to a food source by growing toward it. Fungal growth is mainly confined to the tips of the hyphae. Some mycelia can grow up to a kilometer a day. When one of the hyphae contacts a food supply, the entire secondary cell colony mobilizes and relocates resources to exploit the new food. If all food is depleted, production of spores is triggered. Another form of distribution of the individual cell progression in space is fragmentation of a mycelium. Colonies of different individual cell progressions superpose each other and communicate chemically via pheromones especially prior to mating.

Phylum Chytridiomycota

Chytridiomycota are poorly studied. Some are known to have zygotic meiosis. Some are unicellular, some produce solitary hyphae, and others produce mycelia. They have flagellated gametes. In genus *Allomyces* (Barr DJS 1990, Raven PH *et al* 1999), for example, the zygote propagates and produces the digenomic sporophyte. The sporophyte grows by branching and clones itself by production of digenomic zoospores.

Each mature sporophyte develops sporangia which become released and after a period of dormancy produce monogenomic zoospores by meiosis. After germination, each monogenomic zoospore produces gametophyte. The mature gametophyte produces gametes of both types, male and female. By syngamy, gametes produce biflagellate zygote which, however, loses both flagellae and begins to propagate.

#### Phylum Zygomycota

A zygospore is a chimerical plasmodium containing a number of monogenomic nuclei of two mating types (Raven PH *et al* 1999). It has a period of dormancy before nuclei pair and fuse. Then, digenomic nuclei immediately undergo meiosis and zygospore germinates. Germination involves development of one or more sporangiophores with sporangia at their tips. Sporangia release monogenomic spores each of them gives rise to its own mycelium. With little cellular differentiation among mycelium, hyphae specialize for various functions. Stolons are horizontal hyphae that exist on the surface of the food. Rhizoids are hyphae that grow into the food and carry out digestion. Sporangiophores are stalks that bear sporangia where spores are produced. If released, spores are dispersed by air current and give rise to new mycelia contributing to distribution of the tetradic cell progression in space. Sometimes, two hyphae of different mating types are chemically attracted and grow toward each other. Ends of hyphae swell as nuclei enter. Cross walls without pores develop behind each end, forming multinucleate gametangia. Both gametangia merge into a single chimerical plasmodium which develops a thick wall forming a zygospore. The zygospore remains attached between both parental hyphae during period of dormancy.

#### Phylum Ascomycota

If a plasmodial ascogonium receives nuclei from a plasmodial antheridium through a cytoplasmic bridge, it becomes a single chimerical plasmodium containing numerous nuclei of two mating types (Borkovich KA *et al* 2004, Coppin E *et al* 1997, Kronstad JW and Staben C 1997, Raven PH *et al* 1999, Saupe SJ 2000). Within this plasmodium, nuclei of two mating types pair but do not fuse. They exist side-by-side and propagate synchronously. Plasmodium develops a compact colony of chimerical plasmodial hyphae surrounded by an ascocarp. Walled-off tips of some hyphae become large dikaryotic cells. After its monogenomic nuclei fuse, the cell becomes a meiocyte where the digenomic nucleus undergoes meiosis and each tetrad then undergoes one mitotic division. The cell becomes an ascus, a finger-shaped plasmodium containing eight monogenomic nuclei. Within ascus, each nucleus becomes surrounded by a separate cell wall and differentiates into an ascospore. Ascus swells and bursts, expelling ascospores. At the time they are released, the thick-walled ascospores are resistant to adverse environments. Given the right conditions, the ascospore germinates and develops a mycelium. In mycelium, some aerial hyphae can differentiate into conidiophores which tips contain conidiospores. Conidiospores contribute to distribution of the tetradic cell progression in space. If two hyphae of different mating types are attracted to each other, they differentiate into an ascogonium and an antheridium respectively and form a cytoplasmic bridge through which all the nuclei of the antheridium enter the ascogonium.



In subphylum Saccharomycotina (yeast), cells are usually dispersed in space, but, in response to nitrogen limitation and abundant fermentable carbon source, cells of the zygotic cell progression can undergo transition to filamentous growth (Lengeler KB *et al* 2000, Wittenberg C and La Valle R 2003). The filamentous growth represents a dramatic change in the normal pattern of cell growth in which the cells become elongated, switch to unipolar budding pattern, remain physically attached to each other, and invade the growth substrate. Related transition to filamentous growth occurs also in tetradic cell progressions but rather in nutrient-rich environment. In the tetradic cell progression, cells essentially represent gametes that are short-lived in nature. An elaborate pattern of axial budding has evolved in these cells and is thought to promote rapid mating. Thus, while the role of transition to filamentous growth in zygotic cell progression may be to forage for nutrients, the role in tetradic cell progression may be to forage for mating partners.

### Phylum Basidiomycota

A dikaryotic zygote gives rise to a mycelium. In hyphae, septa separate dikaryotic regions from each other (Casselton LA and Olesnick NS 1998, Hibbett DS and Binder M 2001, Kronstad JW and Staben C 1997, Kües U 2000, Raven PH *et al* 1999). In apical region of the hypha, nuclei propagate synchronously whereby one of the nuclei divides in the main axis of the hypha, while the other divides into a hyphal branch, a clamp. Septa are formed across each of the mitotic spindles so that the new subapical region and the clamp become monokaryotic. If the apex of the backward growing clamp fuses with the new subapical region, dikaryotic condition is reestablished. The mycelium continues its existence for years, perhaps even hundreds of years. Production of conidiospores is rare. Conidiospores may be released either passively or forcibly. Also fragmentation of the mycelium can take place. Occasionally, the mycelium develops one or more basidiocarps. Basidiocarp is a fruiting body such as mushroom or puffball composed of tightly packed hyphae whose walled-off ends become club-like basidia. If walled-off by a complete septum, the end of the hypha becomes a large cell where both nuclei fuse and digenomic nucleus undergoes meiosis. The cell becomes a basidium by forming four projections each of which obtains its own monogenomic nucleus and develops into a basidiospore. Also basidiospores may be released either passively or forcibly. After germination, each basidiospore forms its own mycelium. Monogenomic mycelium is short-living. If two hyphae of different mating types are attracted to each other, their apical regions fuse together producing a dikaryotic zygote. Rapidly growing new dikaryotic mycelium remains attached to parental monokaryotic mycelia.

### Unikonta: Opisthokonta: Microsporidia

Microsporidia are parasites which hosts are representative of almost all invertebrate animal phyla (Canning EU 1990). Karyokinesis often produces a spherical or filamentous plasmodium. Nuclei may be isolated or paired in a dikaryon arrangement. The nuclear envelope remains intact during karyokinesis. Plasmodium may divide by simultaneous fission into smaller multinucleate plasmodia or dikaryotic cells. The plasmodium development culminates in karyogamy producing digenomic nuclei which immediately undergo meiosis. Monogenomic nuclei propagate until the plasmodium

becomes a sporont producing spores. Spores are highly characteristic with a polar tube which is everted in the hatching process and allows the passage of the sporoplasm through it so that the host cell is infected by inoculation.

Unikonta: Opisthokonta: Nucleariida

In Nucleariida, multinucleate plasmodium with sharply pointed fine radiating pseudopodia actively moves varying in form and shape. Sometimes, it becomes a spherical. Number of nuclei per plasmodium ranges from 4 to 80. Nuclear envelope remains intact by karyokinesis.

Unikonta: Opisthokonta: Choanoflagellata

Although considered the closest relatives of Animalia, Choanoflagellata are not yet thoroughly studied (Buck KR 1990, Maldonado M 2004, Nielsen C 2001). It is even not known whether they are monogenomic or digenomic. The cell typically has a funnel-shaped contractile collar of cilia surrounding a single flagellum. Often, cells remain in hypha-like or sphaera-like association and show a limited degree of differentiation. In hypha-like association, cells are usually clustered at end of a simple or branching stalk. Sphaera-like associations, such as of genus *Sphaeroeca*, have collars on the outer side of the sphaera, but others, such as of genus *Diaphanoeca*, have collars facing the interior of the sphaera. Of special note is a sphaera of genus *Proterospongia*, which external cells are typically flagellated and ciliated, but internal cells are non-motile. *Proterospongia* may be the direct ancestors of Porifera.

Unikonta: Opisthokonta: Animalia

The evolution of individual cell progressions of Animalia clearly involved the development of considerable diversification of cells within the cell association.

In Animalia (Gilbert SF 2000, Nielsen C 2001), the zygote propagates by cleavage so that the cells become more and more smaller. Then, the cell association grows and develops in a large variety of ways, forming an initial body with a species-specific primary body plan. This initial body usually clones itself giving rise to an expanding population of primary cell colonies that often remain attached to each other, forming a larger cell association with a species-specific secondary body plan. The secondary cell colony may show differentiation of primary cell colonies. Soon or later, the onset of meiosis is triggered. The tetrads may propagate forming an association of monogenomic cells, but this case is extremely rare. Mostly, the tetrads do not propagate but differentiate into eggs or sperm. The egg usually develops only from one of the tetrads, while the other three become polar bodies and rather degenerate.

Each primary cell colony may frequently change from a free-swimming stage to a sessile stage. In addition to the settlement, this change may include more or less dramatic transformation of the primary body plan. The cloning and formation of secondary cell colony may occur from both the free-swimming stage and sessile stage. In some species, the free-swimming stage is restricted to the initial primary cell colony which soon or later settles and irreversibly transforms into the sessile stage.

Similarly, each secondary cell colony may frequently change from a free-swimming stage to a sessile stage and this change may include more or less dramatic transformation of the secondary body plan.

Generally, most specialized cells can de-differentiate into primordial cells or even re-differentiate into other cell types.

## Formation of animal body plans

While the morphological diversity of animal cell associations seems to be overwhelming, the underlying body plans are nevertheless governed by rather few general principles.

The primary body plan is always a sphaera or its derivative. The sphaera which can be topologically described as the simplest closed surface, with two sides and no boundary lines, can give rise to more complex closed surface such as solenoid or even to a system of solenoids, some embedded in another.

The secondary body plan is a series of primary body plans. However, the serial arrangement may become not more evident.

In contrast to the abstract mathematical surface, the real biological surface is made up not by dimensionless points but by three-dimensional matrix with embedded cells. So, although the biological surface, like the mathematical surface, is with two sides and no boundary lines, it is actually a wall, since there is a distance between its two sides so that these two sides enclose a space with a volume. In other words, whereas a mathematical surface has no thickness, the biological surface does have. The thickness of the wall may have regional differences in magnitude. Additionally, the two sides of the wall can be differently designated according to their orientation to interior or exterior of the body.

Thus, it is very important to recognize that the description of the animal body plan can be generally given in terms of a closed and orientable wall, without boundary lines and with two distinguishable sides. That side of the wall which is oriented into the exterior of the body is here designated as an outside, and that which is oriented in the interior of the body is an inside. One must be aware that the space, which seems to be the interior of the body at the first glance, is actually the exterior.

Within the wall, some cells may become polarized cells arranged in cell layers. Some cell layers may be described as the closed surfaces, but their local orientation may greatly deviate from the direction of the wall orientation, giving rise to the internal complexity of the wall. Additionally, other cell layers may not be described as closed surfaces at all. So, the underlying principles of surface topology remain valid only at the wall level but not at the level of separate cell layers.

The complexity of the primary and secondary body plan enhances gradually at different ontogenetic and phylogenetic stages, providing insight into the most basic directions of animal evolution.

### A. Sphaera as a primary body plan

In early part of animal phylogenesis, the primary body plan corresponds to the three sphaera types: a morula, blastula, and gastrula.

Similar to many other Karyota, ancestral Animalia were able to form a small spherical cell association, the morula, within which the ciliated cells were held together by a semi-fluid extracellular matrix. The morula was without polarity and rolled throughout the water. In extant animal phyla, the morula is retained only as a transitory stage during development of the initial primary cell colony.

The next sphaera derivative, the blastula, evolved when the outermost cells came into close contact to each other forming junctions between cells so that the innermost compartment of the wall was isolated more or less completely from the exterior. This division of the wall into an innermost and outermost compartment had the advantage of a regulated interior, providing the cell association with a higher degree of independence from environment. The blastula then evolved a preferred direction of swimming, establishing an anterior-posterior polarity of the body which was associated with a division of labor between cells of the outermost compartment of the wall. At the anterior pole, the cells with longer cilia formed the most ancestral sensory organ, the apical organ. Around the posterior pole, the more advanced blastula evolved a ring of compound cilia to enhance the power of swimming. This ring, usually called the archaeotroch, was also capable to capture larger food particles and transfer them to the leeward side at the posterior pole where the cells lost the cilia at all. Although distinct parts may be distinguished in the blastula wall, it remains an integumental.

The gastrula came into existence when the wall of the blastula posteriorly to the archaeotroch bent inwards, forming a sac with more or less expanded cavity, the archenteron, which then functioned as a primitive gastral space. The archenteron offered the possibility of the retaining, absorbing, and digesting larger food particles, enhancing thus the food uptake. Although the archenteron formation is achieved by drastic change of a local curvature of the wall, it remains uninterrupted. However, in contrast to the morula and blastula, two main regions of the wall, the integumental wall and gastral wall, are to be distinguished in the gastrula.

In Porifera (Amano S and Hori I 1996, 2001, Bavestrello G *et al* 2002, 2003, Bonasoro F *et al* 2001, Boury-Esnault N *et al* 2003, Degnan BM *et al* 2005, Gallissian MF and Vacelet J 1992, Hill MS and Hill AL 2002, Leys SP 1999, 2003, Leys SP and Degnan BM 2001, 2002, Manconi R and Pronzato R 1991, Nielsen C 1998, 2001, Reiswig HM and Miller TL 1998, Uriz MJ *et al* 2001, Woollacott RM 1993), the cleavage usually leads to direct formation of the blastula with the anterior-posterior polarity. The innermost compartment of the wall is filled by semi-fluid matrix with loosely arranged cells. In some species, it is completely cell-free. In the outermost compartment, the cells are arranged in an epithelium-like layer and become apically ciliated, except the posterior pole. Sometimes, cilia are first oriented into the cell-free interior and the blastula must turn inside out through an opening between cells. The blastula is a free-swimming stage of the initial primary cell colony. It swims by beating of cilia, but soon or later settles with anterior pole against the substratum and irreversibly transforms into a sac-shaped sessile stage, a sponge, with an expanded cavity, the atrium, which opens upward. The margin of the atrial opening is a boundary between two distinct parts of the integumental wall, the feeding wall and atrial wall, which attach each other by their inside surfaces so closely that the double-walled nature of the sac is not more evident. In the sponge wall, the innermost compartment is filled by the primordial cells,

archaeocytes, which produce the semi-fluid matrix, a mesohyl, and spicules. Sometimes, archaeocytes must differentiate into more specialized sclerocytes to be able to produce spicules. Archaeocytes also differentiate into flattened cells, a pinacocytes, some of them contain contractile fibers. Pinacocytes arrange into a non-sealed epithelium-like bilayer, composing the outermost compartment of the feeding wall, and into a monolayer, forming numerous water canals running through both walls. Further, archaeocytes differentiate into characteristic cells, the choanocytes, with a funnel- or tube-shaped collar of long villi surrounding a longer cilium. Choanocytes are usually arranged into well-defined epithelium-like layer, composing the outermost compartment of the atrial wall. The undulating movement of the cilium propels water away from the cell body, thus inducing water current between villi into the collar. The water currents induced by all choanocytes create flow of water through canals. The water enters canals through numerous pores in the feeding wall and leaves through numerous pores in the atrial wall and then through atrial opening. Food particles are captured both by pinacocytes and by choanocytes. They engulf food particles from the water, digest them in vacuoles, or pass them to archaeocytes which transport nutrients from cell to cell. The wall of the sponge is loosely organized. The cell junctions occur only occasionally between the archaeocytes, when some of them arrange together to produce spicules, for example. At the sessile stage, the initial primary cell colony clone itself by fission or budding, giving rise to an expanding sessile secondary cell colony, respectively. Very often, the formation of secondary cell colony proceeds without any sign of fission or budding so that the initial sponge develops into a growing massive sponge colony of a sycon or leucon type, with an intricate net of common water canals and numerous choanocyte chambers. In any cases, special resting stages, gemmulae, contribute to distribution of individual cell progression in space. Gemmulae can survive extremely unfavorable conditions that cause the rest of the sponge colony to die. Archaeocytes and choanocytes can undergo meiosis producing gametes. Eggs and sperm are produced at different times. Eggs develop either from archaeocytes or from choanocytes which lose their collars and move into the matrix. Sperm develop from choanocytes only. In the sponge colony, the whole choanocyte chamber can become transformed into sperm which is shed into the chamber lumen and expelled from the colony through common water canals. When single sperm enters another sponge, it becomes trapped by an archaeocyte and transported to an egg in the matrix to form a zygote. Development of new initial primary cell colonies takes place inside the maternal sponge in almost all Porifera species.

In Cnidaria (Ball EE *et al* 2002, Barneah O *et al* 2002, Blackstone NW *et al* 2004, Cartwright P 2003, Dahan M and Benayahua Y 1998, Davy SK and Turner JR 2003, Freeman G 2005, Gröger H and Schmid V 2001, Gutiérrez-Rodríguez C and Lasker HR 2004, Isomura N *et al* 2003, Kossevitch IA *et al* 2001, Lasker HR *et al* 2003, Martin VJ 2000, Nielsen C 1998, 2001, Weis VM *et al* 2002, Yamashita K *et al* 2003), the cleavage usually leads to the formation of the blastula which then elongates and becomes a flat, pear-shaped planula. Cells are held together by semi-fluid extracellular matrix. The innermost compartment of the wall may contain loosely arranged cells or may be completely cell-free. In the outermost compartment, cells are apically ciliated. At the anterior pole, cells develop longer cilia and become sensory, forming an apical organ. The planula is the free-swimming stage of the initial primary cell colony. At the posterior pole, the wall often bends inwards to form the more or less expanded

archenteron, making the planula planktotrophic. The planula usually settles with the anterior pole, attaches to the substratum, and becomes a flat primordial disk. All specialized cells become rather absorbed and ingested by primordial cells which propagate and begin to produce a gelatinous to almost cartilaginous, hyaline matrix, the mesoglea. The primordial disk expands in a variety of ways. The lower side develops into a pedal disk. At the upper side, a circular fold of the wall usually stretches upwards forming a sac-shaped polyp with an expanded cavity which then functions as a new gastral space. A ring of tentacles with extensions of the gastral space surrounds the sac opening. The next circular fold extends from the sac opening into the gastral space. Longitudinal folds, mesenteries, may extend radially. Although the relation of the new gastral space to the archenteron is uncertain, the two main regions of the polyp wall, the integumental wall and gastral wall, may be clearly distinguished. Their innermost compartments fuse to a thin sheath which, however, may locally swell and even contain cells. Cells of the outermost compartment are anchored to the basement membrane and form an uninterrupted sealed layer within which the primordial interstitial cells differentiate mostly into the tall cells, a myoepitheliocytes, containing muscle fibers at the base. The fibers interconnect longitudinally in the integumental wall and circularly in the gastral wall. Thus, there are two antagonistic muscle layers in the polyp. Numerous sensory, nervous, secretory and other specialized cells are scattered between myoepitheliocytes. Most characteristic are however cnidocytes. A cnidocyte contains nematocyst, a fluid-filled capsule with a long spirally coiled hollow thread. When the trigger of the cnidocyte is touched, the nematocyst is discharged. Some threads trap prey or predator, some have spines to penetrate and inject paralyzing toxins. Nervous cells interconnect to form a neural plexus which transmits impulses in several directions at once, resulting in multiple firing of nematocysts in body parts not directly stimulated. Both nerve and muscle fibers enable polyp for directional movement. The polyp can contract or extend. Tentacles can extend to grasp prey. In the gastral wall, cells secrete digestive juices. In the integumental wall, cells can secrete an external cuticle. Although sedentary, polyp is not completely sessile in most species. Some can glide from place to place on the pedal disc. Others can crawl on the side of the body or even walk on the tentacles. By fission or budding, the initial polyp gives rise to a growing number of polyps which often remain attached to each other and form an expanding secondary cell colony. In some species, the colony of polyps may be enclosed in a hard, chitinous covering. In the colony, polyps may differ structurally and functionally. Primordial cells can undergo meiosis producing gametes. Both eggs and sperm are usually shed freely in the water. In some species, polyp fragmentation can bring forth specialized free-swimming stages, medusae, which then produce and disperse gametes. In any species, the free-swimming planula develops direct into the medusa. The medusae are able to clone themselves too.

In Ctenophora (Henry JQ and Martindale MQ 2004, Nielsen C 1998, 2001, Sullivan LJ and Gifford DJ 2004), the cleavage leads to the formation of a blastula which then becomes a very delicate sac-shaped free-swimming body with an expanded archenteron and a pair of tentacles. Thus, two main regions of the wall, the integumental wall and gastral wall, may be clearly distinguished. The spacious innermost compartment of the wall, contains predominantly a gelatinous hyaline matrix, a mesoglea, and a few smooth muscle cells and mesenchymal cells. The smooth muscle cells are very large and branched. In the outermost compartment of the wall, the cells are arranged in an

epithelium. Between both compartments, there is a conspicuous basement membrane. Externally, the body typically looks as a spherical or ovoid, but may become extremely flattened in the tentacular plane. In the integumental wall, the epithelium is first monolayered but, later, it becomes separated in an external layer of ciliated cells, with sensory and secretory cells scattered between them, and an internal layer of nerve and muscle cells. A dome-shaped cap with specialized sensory cells protrudes from the anterior pole. In some species, however, these sensory cells are situated rather in a small anterior cavity. Below the anterior cap or cavity, there is usually a concentration of nerve cells in the integumental epithelium. The integumental wall may form folds or lappets. Eight meridional rows of large fused cilia, a comb plates, are the only locomotory organs of the body so that the typically weakly swimming of the body is largely at the mercy of the prevailing water currents. The presence of combs is just the most distinctive feature of the phylum, giving its name. The tentacles are cylindrical and often have numerous side branches. The tentacles are muscular and can be retracted into the sheaths. The tentacular epithelium bears very characteristic cells, a colloblasts, which are formed continuously from undifferentiated interstitial cells of the basement growth zone. Apically, the colloblast has numerous granules which release sticky mucus substance by contact with a prey. The opening of the archenteron is a narrow slit which leads through a large flattened pharynx into a rather small stomach. The pharyngeal plane is transverse to the tentacular plane, establishing the so called biradial symmetry of the body. A narrow aboral extension of the stomach leads to a pair of canals with an extremely precise branching pattern so that, in addition to the main aboral canal, there are usually a pair of transverse canals, two pharyngeal canals, two tentacular canals, and eight meridional canals along comb plates. The gastral epithelium is composed of both ciliated and phagocytic cells. Digestion begins extracellularly but is completed always intracellularly. The free-swimming body grows continuously. In few species, it settles and becomes sessile. The cloning and formation of secondary cell colony have never been observed. However, Ctenophora are known as having a substantial capacity for regeneration. They are able to regenerate lost part: once used to capture prey, a tentacle is usually lost and subsequently regenerated. They may regenerate the whole body even from a small fragment. Gametes are produced in meridional canals and shed through numerous tiny pores in the comb plates. Each body usually produces both eggs and sperm, but in separate canals. The egg is usually connected with three clusters of nurse cells through intercellular bridges.

#### B. Sphaera-in-sphaera as a primary body plan

The opening of the archenteron may close partially or completely forming a solenoid or sphaera-in-sphaera, respectively. Since the solenoid formation may be achieved by the partial closure of the archenteron and by transitory interruption of the wall, the solenoid at the first glance seems to be more ancestral primary body plan than the sphaera-in-sphaera. But, in the ontogenesis of many extant animal phyla, rather the sphaera-in-sphaera formation precedes the solenoid formation. It may even precede the gastrula formation as the ontogenesis of some Cnidaria shows. Additionally, one of the most basal animal phyla, Placozoa, possibly retained the sphaera-in-sphaera as a primary body plan. Taken together, these facts suggest that the sphaera-in-sphaera may be more ancestral primary body plan than the solenoid.



The phylum Placozoa comprises only one known individual cell progression species, *Trichoplax adhaerens*, which life history has never been studied in any natural habitat and is known very fragmentary (Ender A and Schierwater B 2003, Maruyama YK 2004, Thiemann M and Ruthmann A 1991). Zygote formation and propagation were not observed. The best known stage, kept alive in various laboratories, is a sphaera which is so extremely flattened that it looks as a double-walled disk creeping on substratum in warm water. Therefore, two main regions of the wall, the lower wall and upper wall, are usually distinguished. Their inside surfaces attach each other so closely that the double-walled nature of the disk is not more evident. The innermost compartment of the wall is filled by a gelatinous matrix with a meshwork of star-shaped fibre cell. The fibre cells are tetraploid, contain actin filaments, and are therefore responsible for the sometimes quite rapid changes of the body shape. In the outermost compartment of the wall, the ciliated cells are arranged in an epithelium-like layer. At the lower wall facing substratum, the ciliated cells are rather tall cells between which some secretory cells are scattered. At the upper wall, the layer contains flat ciliated cells and spectacular cells with inclusions originating from degenerating cells. The body clones itself by fission, by budding, or by formation of secondary free-swimming stages, the swarmer. The swarmer consists of two concentric walls surrounding a central lumen and is therefore a sphaera-in-sphaera. When the swarmer settles, it opens at one side and stretches out so that the lower and upper walls become established by inner and outer walls respectively. Meiosis was not observed. Eggs seem to be formed in the lower wall and become surrounded by fibre cells which function as nurse cells. In culture, eggs form fertilization membrane and start to divide, but the progeny cells soon disappear.

### C. Solenoid as a primary body plan

The blastula may transform into either gastrula or sphaera-in-sphaera which both can convert into each other and both can give rise to the solenoid. So, there is a variety of ontogenetic ways of solenoid formation which phylogenetic interrelationships remain unclear. If the gastrula is a preceding stage, the solenoid may be formed either by a partial closure of the archenteron opening leaving two openings or by the formation of an additional invagination which then fuses with archenteron to produce the second opening. If the sphaera-in-sphaera is a preceding stage, the solenoid formation requires the establishment of two new openings.

The tube between two openings of the solenoid functions as a gastral tube, the gut, which lumen represents the exterior in relation to the body. It may extend and branch in complex ways without affecting the solenoidal topology of the wall. The food particles pass the gut lumen only in one direction from one opening, the mouth, to the other, the anus. The origin of different gut regions depend greatly on the way by which the solenoid is formed and varies between the most phyla.

In addition to the anterior-posterior polarity, the solenoid developed a dorsal-ventral polarity and became bilateral symmetric. However, one must be aware that the anterior-posterior axis may deviate from the ancestral orientation depending on the way of solenoid formation.

Generally, the innermost compartment of the wall remains filled predominantly by the semi-fluid matrix with only few cells. Some of these cells arrange in a pair of branched canals which open into a posterior cavity, the cloaca. The branches terminate with specialized cells which function as a protonephridia. The outermost compartment of the wall remains predominantly the myoepithelium. Numerous sensory, nervous, secretory and other specialized cells are mostly scattered between myoepitheliocytes, but may form local concentrations as well. Both compartments of the wall are usually separated by a basement membrane. The two main regions of the wall, the integumental wall and gastral wall, become more elaborated and develop a variety of specialized regions. The apical organ usually persists, but its location depends greatly on the way of solenoid formation. Numerous ciliary bands are formed, but their relation to the archaeotroch is not clear.

A large number of extant animal phyla retained the solenoid as a primary body plan of the initial body.

In Rotifera (Birky CW 2004, Fontaneto D *et al* 2003, Gilbert JJ 2003, Gomez A and Carvalho GR 2000, Nielsen C 2001, Schröder T 2003, Serra M *et al* 2004, Wallace RL 2002, Welch DBM and Meselson MS 2001, Welch JLM *et al* 2004), the initial free-swimming body is solenoid-shaped. The innermost compartment of the wall contains predominantly semi-fluid matrix but also a pair of branched canals which open into the cloaca. The branches terminate with specialized cells, the flame cells, functioning as a protonephridia. The outermost compartment of the wall is the myoepithelium which becomes plasmodial in many regions. The integumental wall develops a variety of structures such as ciliary rings, ridges, pits, papillae, and bristles. The wheel-shaped anterior region with one or more ciliary discs, a corona, becomes the most distinctive feature of the phylum, giving its name. Cuticular plates encircle the body forming a protective lorica. The posterior aspect of the body typically narrows forming a retractile foot. Food particles captured by the corona are transported through the ciliated buccal tube to the muscular pharynx, a mastax, which contains hard chitinous jaws and chews ceaselessly. The particles are crushed and manipulated before being passed into the ciliated oesophagus, where the preliminary digestion occurs, and then into the stomach which may be either cellular with cilia or plasmodial without cilia. There is usually a pair of gastric glands, but some few species have four gland pairs and one unpaired elongated gland. Short ciliated intestinal tube opens into the cloaca. As a species-specific number of cells or nuclei is reached, the cell division becomes restricted to the highly determined subset of the cells within the innermost compartment of the wall and is used by the initial body to clone itself, developing an expanding population of new bodies. The life span of the body is usually around 1 to 2 weeks. In some species, bodies of homogenous or heterogeneous age remain in a free-swimming secondary cell colony embedded in a common gelatinous matrix. Both the solitary and colonial bodies may settle down and become sessile, attaching to the substratum by foot. Sessile bodies actively sway from side to side and contract frequently. The population continues to expand until deteriorating conditions stimulate the onset of the meiosis within the subset of dividing cells, producing tetrads. Some of them are actually eggs and wait to be fertilized, but other tetrads propagate and each develops into a monogenomic dwarf male with vestigial, non-feeding gut. In the male, most cells differentiate into sperm and oversized copulatory organ. Fertilization produces a dormant zygote which is highly

resistant and may remain quiescent for months or years. In most species, however, the meiosis, male development, and fertilization have never been observed, since the population survives unfavorable condition rather by cryptobiosis and may remain in this stage for months, years, or even a century. The recovery requires 10 minutes to several hours. Thus, some Rotifera species retain the most ancestral type of the life history of the individual cell progression, being able to form cell associations not only within the zygotic cell progression but also within the tetradic cell progressions.

In Cyclophora (Kristensen RM 2002, Obst M and Funch P 2003), which comprise only one known individual cell progression species, *Symbion pandora*, the free-swimming stage of the initial body, a chordoid, is solenoid-shaped. In the wall, the thin innermost region is filled with semi-fluid matrix and is cell-free. The outermost compartment is a myoepithelium. The chordoid usually settles on the bristle surrounding mouth of the lobster, becomes eventually attached to it, and transforms into a sessile feeding stage of the initial body. From the attachment disc, a short stalk develops. At the stalk, there is a main trunk with a U-shaped gut which mouth and anus lie close to each other and are directed upwards. Around the mouth, a circular fold expands into a bell-shaped buccal funnel with a ciliated margin. The gut has well-defined oesophagus, stomach and rectum regions. The buccal funnel and gut continually degenerate and are replaced by internal budding. The sessile body clones itself: a special stage, a pandora, with a miniature sessile body is continuously produced in special brood chamber, escapes and immediately attaches nearby so a large population of feeding stages arises. Triggered by the imminent molting of the lobster host, the body of either male or female type is developed by internal budding. The significantly smaller male body is a simple sac without buccal funnel and gut. It breaks free, matures to produce two stores of sperm and two copulatory organs, and then attaches to the sessile body which is in the process of producing a female body. In the female body, only one tetrad differentiates into the egg. After its single egg is fertilized, the female body eventually breaks free and settles nearby. The zygote develops into the chordoid within a female body which progressively degenerates allowing the chordoid to escape and swim to new host.

In Micrognathozoa (Kristensen RM 2002, Kristensen RM and Funch P 2000, Sorensen MV 2003), which comprise only one known individual cell progression species, *Limnognathia maerski*, the initial free-swimming body is solenoid-shaped, but the gut has only a temporary anus of interdigitating integumental and gastral cells. The innermost compartment of the wall is filled by semi-fluid matrix with few muscle cells and contains two pairs of protonephridia. The outermost compartment is a mono- or multiciliated epithelium. At the dorsal and lateral side of the body, the integumental myoepitheliocytes produce intracellular skeletal plates. At the ventral side, cells bear compound cilia and are the chief locomotory organ. Pharyngeal cells secrete cuticular jaws which are similar to those of Rotifera. The cloning, meiosis, fertilization, and development have not been observed, but there are numerous indices that Micrognathozoa may be similar to Rotifera also in this respect.

In Gnathostomulida (Herlyn H and Ehlers U 1997, Nielsen C 2001), the gut is blind, but some species have a temporary, periodically functional, anus of interdigitating integumental and gastral cells. The innermost compartment of the wall contains muscle cells. There are also 2-5 pairs of protonephridia. The outermost compartment is a

monociliated epithelium. Pharynx is equipped by cuticular jaws similar to those of Rotifera and Micrognathozoa. During the body life history, the onset of meiosis is triggered many times so that the juvenile stages alternate with adult stages, reliving periods of maturity over and over again. The body produces gametes of both types but in separate regions. Fertilization occurs internally with production of a single large zygote which then breaks directly through integumental wall to escape from the body. Remarkably, the cleavage exhibits a spiral pattern.

In Kamptozoa (Entoprocta) (Nielsen C 1998, 2001, 2002a, Wasson K 1998), the free-swimming stage of the initial body, a trochophore, is solenoid-shaped. The innermost compartment of the wall is filled by semi-fluid matrix with a few cells arranged in a pair of branching canals. Each canal usually has three branches terminated with a multiciliated cells functioning as a protonephridia. The outermost compartment is a ciliated myoepithelium. The body is named a trochophore for the wheel-like appearance of the two main bands of compound cilia: a large prototroch which girdles the body around the middle and a smaller metatroch which is just below the mouth and parallel to the prototroch. In most species, the trochophore has a large retractable frontal organ with concentrations of sensory, nervous, and secretory cells. Between both openings of the U-shaped gut, there can be also a foot with three pairs of sacs filled by an adhesive secretion. The trochophore usually swims only few hours before it settles and, when it is ready to settle, it usually creeps on the substratum on the foot and tests it with the frontal organ. When a suitable spot has been found, the trochophore settles on the foot which sacs turn inside out and give off their content. The hyposphere is retracted so that it envelopes the body completely forming a closed atrium. The body becomes attached to the substratum with the ring-shaped zone. Most of the trochophore organs disappear, but the gut persists and rotates about 180°. The depressed ventral side with the mouth above the anus becomes surrounded by tentacle buds. Then, the atrium opens exposing short tentacles. The body stretches upwards. The region attached to the substratum develops into a shorter or longer cylindrical stalk carrying the main trunk. Tentacles carry characteristic bands of cells with longer cilia. There are numerous lateral concentrations of sensory cells. At the bottom of the atrium, nervous cells concentrate into a dumbbell-shaped ganglion which connects with a fine nervous net of the body. Within the innermost compartment of the wall, the cells reestablish a new pair of branching protonephridial canals which open at the bottom of the atrium. The sessile body secretes a thin chitinous cuticle which is however quite thick at the stiff portion of the stalk. The initial body clones itself giving rise to an expanding secondary cell colony. At maturity, additional paired canals develop in the innermost compartment of the wall and open at the bottom of the atrium. Each canal usually connected with one or two sacs within which gametes are produced. Eggs are retained, sperm is shed. Fertilized eggs become attached exteriorly to the atrium surface where developing trochophores are retained for a period. The cleavage is spiral.

In Priapulida (Lemburg C 1998, Nielsen C 2001), the initial free-swimming body is a solenoid-shaped. From exterior, it looks as an elongated cylinder which anterior part becomes a large introvert, carrying many rings of specialized spines. In some species, there are tentacles around the mouth. The spacious innermost compartment of the wall is filled by semi-fluid matrix and contains muscle cells, erythrocytes and amoebocytes. There is also a pair of canals with numerous protonephridial branches. Canals open

lateral to the anus. The outermost compartment of the wall is a myoepithelium. The integumental epithelium secretes a chitinous cuticle and spines. The pharynx contains circles of cuticular teeth. The free-swimming initial body may develop caudal appendages to anchor the sediment. The growth is accompanied by periodic molting. Adult stages show a male-female dimorphism, producing either eggs or sperm. Gametes are produced in the innermost compartment of the wall and shed through common protonephridial canals.

In Kinorhyncha (Neuhaus B and Higgins RP 2002, Nielsen C 2001), the initial free-swimming body is solenoid-shaped. From exterior, it looks as an elongated cylinder tapering towards the posterior end. The anterior part of the body is an introvert with a retractable mouth cone. Small stylets surround the mouth. The median part of the introvert carries many rings of specialized spines. The mouth cone can be retracted inside the introvert which in turn can be retracted into the trunk. The innermost compartment of the wall contains muscles and amoebocytes. A pair of protonephridia is present. The outermost compartment of the wall is an epithelium which may be plasmodial. The integumental epithelium secretes cuticle and spines and the growth involves a number of molts during which time a characteristic segmental arrangement of cuticular plates, spines, and muscles is acquired. There is usually a male-female dimorphism of adult stages. Gametes are produced in the innermost compartment of the wall and shed through paired pores situated on the terminal segment.

In Loricifera (Heiner I and Kristensen RM 2005, Kristensen RM 2002, Nielsen C 2001), the initial free-swimming body is solenoid-shaped. Its anterior part houses an introvert with a mouth surrounded by stylets. A specialized system of hardened cuticular plates and spines, a lorica, surrounding the body, gives the phylum its name. There is a varying number of molts. The adult stages show a male-female dimorphism.

In Nematoda (Hodgkin J 2002, Nielsen C 2001), the blastula develops the archenteron with an elongated opening. The lateral opening lips become pressed together and fuse, leaving a large mouth. Later, the small anus is formed, and the body becomes solenoid-shaped and starts to curve. The innermost compartment of the wall contains muscle cells and a few excretory cells. The outermost region contains epithelial or myoepithelial cells and a few sensory, nervous, and secretory cells. Some regions of the wall become plasmodial. The epithelium secretes a thick elastic collagenous cuticle which surrounds the body and also lines the buccal cavity, pharynx, and rectum. The cuticle hardens and must be molted four times to permit growth. As a species-specific number of cells or nuclei is reached, the cell division becomes restricted to the highly determined subset of the cells within the innermost compartment of the wall and is used by the initial body to clone itself, developing an expanding population of new bodies. The body is able to save itself by cryptobiosis, when its environment becomes hostile. If meiosis is triggered, it occurs within a subset of dividing cells. The body first produces sperm and then turns to production of eggs. Fertilization is internal with copulation.

In Nematomorpha (Bohall PJ *et al* 1997, Nielsen C 2001, Schmidt-Rhaesa A 2002), the nematode-like solenoid-shaped body externally looks as an extremely elongated slender cylinder. It is specialized for parasitic lifestyle. The nutrient uptake occurs through integumental wall and the rudimentary intestine is involved in the food storage only.

Some species lack the mouth, and the pharynx is without lumen. The body is surrounded by cuticle which must be molted several times to permit growth. The adult stage is non-feeding. It leaves the host, produces and lays gametes, and dies.

In Gastrotricha (Nielsen C 2001, Weiss MJ 2001), the initial free-swimming body is solenoid-shaped. It is elongated and flattened. The innermost compartment of the wall contains a pair of branching canals. Most branches are terminated by specialized cells, solenocytes, functioning as protonephridia. The outermost compartment of the wall is myoepithelial and mostly plasmodial. The integumental wall is covered by scales and bristles or by cilia which are often grouped in bands and stripes. The adhesive tubules project from the surface of the body, providing short-term attachment to the substratum. The gut is roughly triangular in cross-section. The food is sucked into the mouth by pumping pharynx which in some species has a pair of pores which vent excess water. The cloning is by release of thin-shelled digenomic cells giving rise to rapidly expanding population of free-swimming bodies. If the meiosis is triggered, the body may produce gametes of both types but not at the same time. Fertilization is internal with copulation. The zygote is thick-shelled and dormant. It can remain viable and survives for a long period of time in hostile environment.

#### D. Solenoid-in-solenoid as a primary body plan

There is a variety of ways to transform the solenoid into the solenoid-in-solenoid. The more or less spacious lumen of the internal solenoid, a coelom, which is topologically equivalent to the exterior of the body is filled by fluid. The internal solenoid is usually coiled around the gut, occupying space between the integumental and gastral walls. The wall thus becomes divided into three main regions: the integumental wall, the gastral wall, and the coelomic wall. The portion of the coelomic wall which attached to the integumental wall is usually called a parietal wall, while that which attaches the gastral wall is called a visceral wall. The coelomic wall becomes a principal place of gamete production. The single internal solenoid tends to divide so that more than one internal solenoid is present. However, more typically, a number of paired or unpaired bladders develops in space between the integumental and gastral wall and then gives rise to the internal solenoid-like bladder associations.

In Bryozoa (Ectoprocta) (Bayer MM and Todd CD 1997, Hageman SJ 2003, Hughes RN *et al* 2004, Nielsen C 1998, 2001, 2002a, 2002b, Temkin MH and Bortolami SB 2004, Wendt DE and Woollacott RM 1999), the free-swimming stage of the initial body, a cyphonautes, has a well-developed gut and is planktotrophic. The integumental wall at the posterior pole develops a half-circular fold which extends anterior-posteriorly, surrounding an expanded vestibule. The U-shaped ridge of ciliated cells divides the vestibule into an anterior inhalant and a posterior exhalant chamber. The body soon becomes laterally compressed. The integumental epithelium of the episphere usually secretes two triangular valves. The epithelium of the exhalant chamber develops a large, complicated adhesive sac. The cyphonautes can spend weeks in the plankton, but whether it can clone itself has not been reported. But, when the time is ripe, the cyphonautes creeps on the substratum, explores it and, when a suitable spot has been found, the sac with adhesive secretion turns inside out giving off its content and the cyphonautes becomes attached to the substratum. After settling, the sac expands over

the substratum and the cyphonautes becomes dorso-ventrally compressed by muscle contraction. The shells are released and the episphere expands over the upper side of the body and fuses with the sac border so enclosing all specialized cells which then degenerate. The body becomes a primordial disk which then expands in a variety of patterns to give rise to a sessile stage of the body, a cystid. Cells arrange into two concentric monolayers separated by a common basement membrane. At the upper side, a polyp-like bud, a polypide, develops. First, two invaginations grow and fuse forming an U-shaped gut so that both monolayers become solenoid-shaped. The internal solenoid is coiled around the new gut. Both arms of the gut are directed upwards, the mouth and anus lie close to each other. Then, a ridge with a circle of tentacles, a lophophore, develops around the mouth. The lophophore usually develops two lateral extensions which run in the direction of the anus so that the tentacle crown becomes horseshoe-shaped. The lumen of the interior solenoid, the coelom, expands and sends extensions into tentacles. Thus, three main regions of the wall, the integumental wall, gastral wall, and coelomic wall, may be clearly distinguished. The innermost compartment of the wall is reduced. The outermost compartment is the myoepithelium. Numerous sensory, nervous, secretory and other specialized cells are scattered between myoepitheliocytes. At the posterior side of the mouth, nervous cells concentrate into a ganglion with lateral extensions following the lophophore base. The ganglion connects with a fine nervous net. Tentacles carry characteristic bands of cells with longer cilia. Myoepitheliocytes of the oesophagus can shorten or widen thereby contracting or expanding the oesophagus space. There is often a gizzard with teeth at the entrance into the stomach. Waste products accumulate in the cells of the stomach, the whole polypide degenerates, and the cystid forms periodically a new polypide. The coelom is crossed by muscular folds by which the polypide can be retracted into the cystid which then closes. Whereas the cystid has a sometimes quite thick chitinous cuticle with calcified layers, the polypide cuticle is rather thin. The initial sessile body clones itself by budding so that a large secondary cell colony arises which often shows a specialization of bodies. There are a large numbers of budding patterns and colony forms. The colony largely dies off in winter and regenerates in the following summer. Masses of cells surrounded by chitinous cuticle can remain dormant for some time, withstand unfavorable conditions, and then germinate to regenerate colony. In visceral coelomic wall, primordial cells can undergo meiosis producing gametes which then float in the coelomic fluid. Eggs can be shed into the water but are mostly retained in special chambers. Sperm are usually shed through transitory pores at the tips of the tentacles. Free-swimming sperm can be captured by tentacles and fertilize the eggs. The new cyphonautes develops mainly in a brood chamber in one of a bewildering variety of ways.

In Phoronida (Bartolomaeus T 2001, Nielsen C 1998, 2001, 2002a, Santagata S 2002, 2004), the developing free-swimming stage of the initial body, the actinotrocha, is first solenoid-shaped. Then, some cells enter the space between the integumental and gastral walls and arrange anterior-posteriorly into a series of three bladders which wound into internal solenoids around the gut. The lumina of these solenoids are referred to as a protocoel, mesocoel, and metacoel, respectively. The metacoel communicates with the exterior through pores. When tentacles develop, narrow extensions of the mesocoel enter them. Bands of longer and more closely set cilia develop along the lateral faces of the tentacles and become feeding and locomotory organ of the actinotrocha. Later, a

band of large compound cilia develops around the anus and functions as the main locomotory organ. Just anterior to the anus, the median invagination of the integumental wall develops into a pair of protonephridial canals each with several branches equipped by solenocytes. The common part of the protonephridial canals soon disappears. The protonephridial pores are situated near the pores of the metacoel. In the advanced actinotrocha, solenocytes form clusters and drain the innermost compartment of the wall. Gradually, the actinotrocha develops a complicated nervous plexus with an additional sensory organ which is protruded when the actinotrocha is testing the substrate for settling. If the actinotrocha is about to be ready for settling, a long tubular invagination of the ventral part of the integumental wall, a metasomal sac, develops and occupies much of the space around the gut. At settling, the actinotrocha rapidly transforms. The metasomal sac everts, pulling the gut into an U-shaped. Contractions in the body bring the mouth and anus close to each other and make them both directed upwards. The body stretches up, both arms of the gut extremely elongate and run close to each other. Most cilia and tentacles are either resorbed or cast off and then ingested by the developing sessile body. The main part of the protoceol is lost but it persists, though as a small uncharacteristic lumen. The mesocoel sends extension in new tentacles which grow from small frontal knobs at the base of old tentacles forming usually a horseshoe-shaped row of tentacles, a lophophore. The lophophore bears from ten to several hundreds of tentacles. The arms of the lophophore can be spirally coiled. The metacoelic wall forms numerous mesenteries which suspend the gut. A well-defined plexus of blood canals develop within the gastral and metacoelic wall. Two or three longitudinal blood canals run along the gut which is surrounded by a blood chambers, the lacunae. In tentacles, small blind blood canals are formed in folds of the frontal side of the mesocoelic wall. The terminal protonephridial canals breaks off and become resorbed and ingested, the canals now end blindly. At a later stage, mesocoelic epithelium forms a pair of large funnels which gain connection with the protonephridial ducts to form metanephridial canals. The integumental wall produces cylindrical chitinous tube covered by mud or sand. The initial sessile body clones itself by budding, forming a small secondary cell colony. Gametes are produced within the visceral metacoelic wall near the stomach region. Eggs are usually retained in the mesocoelic extensions in the tentacles. The sperm becomes enclosed in elaborate spermatophores which are shed through metanephridial canals and float in the water. If they are engulfed by lophophores of another specimen, most sperm enter the mesocoel to fertilize eggs.

In Brachiopoda (Lüter C 2000, Nielsen C 1998, 2001, 2002a), the developing free-swimming stage of the initial body is first gastrula-shaped. Then, some cells enter the space between the integumental and gastral walls laterally to the gastral cavity and arrange anterior-posteriorly into a series of coelomic bladders, three or four on each side. The gastral cavity finally closes. Dorsally to each coelomic pair, the integumental epithelium forms a pair of thickenings with bundles of chaetae. Whether the free-swimming stage can clone itself has not been reported. At settling, the body attaches with the posterior pole, where the stalk develops. The mouth and anus break through, and the gut elaborates. The horseshoe-shaped lophophore develops and becomes intricately coiled and wound. Within the innermost compartment of the wall, some cells secrete hyaline matrix and spicules. Two shell valves become secreted from special areas of dorsal integumental wall. These areas expand to an upper and a lower mantle



fold and valves soon enclose completely the whole body and the lophophore. Special muscles open and close the valves. Valves are usually unequal in size. The stalk protrudes through slit between the posterior edges of the valves. The first pair of coelomic bladders disappears. The second pair develops extensions to the lophophore. The third pair becomes a spacious body coelom which sends elaborate extensions into the mantle folds and into the stalk. The fourth pair has not been followed through the transformation. Neural concentration, blood and metanephridial canals become more or less developed. The juvenile sessile stage grows and matures to become an adult sessile stage. Gametes are produced within the wall of the body coelom. There is usually a male-female dimorphism at maturity. Eggs can be spawned free or retained in the lophophore. The sperm is usually shed through the metanephridial canals.

In Sipunculida (Nielsen C 1998, 2001), the cleavage is spiral and the free-swimming stage of the initial body is first a trochophore which then develops a pair of coelomic bladders. Later, the bladders fuse completely surrounding the gut and tentacles develop from the rim of the mouth. In most species, the trochophore develop additional structures and becomes a pelagosphaera which usually has an extended ciliated lower lip with a buccal organ and a lip gland and a retractile terminal organ with sensory and secretory cells. The coelom sends extensions in the tentacles, and a pair of metanephridial canals is developed. The pelagosphaera is a very long-living free-swimming stage, up to one year, and is adapted for long range dispersal by currents, but whether it can clone itself has not been reported. It usually does not settle, but transforms into a free-living juvenile stage which then grows and matures to become a free-living adult stage. The coelom extremely expands and develops numerous canals extending into the integumental wall. Its anterior part with extensions in the tentacles becomes pinched off. The gut becomes U-shaped and forms twisted loops suspended in the posterior part of the coelom. The slender anterior part of the body, the introvert, can be retracted by longitudinal muscular folds of the coelomic wall and everted by contraction of circular muscles. The mouth is terminal to the introvert, the anus is situated at the base of introvert. Metanephridia also become suspended in the coelom. Nephridiopores are situated near the anus. Small cell complexes, the urns, regularly detach from the coelomic epithelium and swim around in the coelomic fluid. They trap and remove particulate debris, and secrete mucus in response to pathogens. Frequently, they travel to the metanephridial funnels and drop collected waste products for excretion. The integumental wall secretes a stiff and very tough cuticle. The free-living body is able to regenerate lost parts of its tentacles, introvert, trunk, or gut. In some few species, it is also able to clone itself by breaking into a large anterior portion and a smaller posterior portion, each capable of regrowing the missing part. Gametes are produced in the visceral coelomic wall and released into the coelom where they mature. Ripe eggs and sperm are selectively collected in metanephridial canals and shed into sea.

In Annelida (Fischer A and Fischer U 1995, Giangrande A 1997, Gibson GD and Smith HL 2004, Halanych KM *et al* 2002, Henderson SY and Strathmann RR 2000, Hansen B 1993, Hardege JD and Bartels-Hardege HD 1995, Licciano M *et al* 2002, Müller MCM *et al* 2003, Nicolaidou A 2003, Nielsen C 1998, 2001, Pernet B 2000, 2001, 2003, Quast B and Bartolomaeus T 2001, Shankland M and Seaver EC 2000, Walters LJ *et al* 1997), the cleavage is spiral and the initial free-swimming body is a primitive

trochophore which usually does not settle but, when the time is ripe, undergoes a cloning by internal budding which involves a rapid addition of new segments, forming a free-living secondary cell colony. The gut stretches out so that the colony becomes a segmented worm with a common gastral tube. In each segment, a gut is surrounded by a pair of coelomic bladders. Thus, three main regions of the wall, the integumental wall, gastral wall, and coelomic wall, may be clearly distinguished. The innermost compartment of the wall contains muscle layers, a plexus of blood canals, and paired protonephridial canals which open into the corresponding coeloms. The outermost compartment is a layer of ciliated epithelium, but many cells are actually myoepitheliocytes. At each segment, the integumental wall develops a variety of paired structures such as appendages, ganglia, and metanephridia. Appendages which are thought to be homologues of the lophophore develop into branched parapodia. Some branches may function as gills. In some species, the appendages at the first segment rather form a ring of tentacles around the mouth. In any other species, they develop into two bundles of numerous slender feather-like gills. Transverse and paired longitudinal nerves connect paired ganglia into a closed nervous system. Metanephridia are shown to be a modified protonephridial canals. The integumental epithelium secretes a collagenous cuticle. Some cells secrete chitinous bristles, chaetae that project from the body. Additionally, the worm may secrete and inhabit a calcareous tube attached to firm substrata. The integumental muscle layers are usually circular. The gut may have a pair of lateral branching diverticula in each segment. The coelomic epithelium produces a fluid in which many cells float. In coelomic epithelium, some cells become chlorogogen. In the coelomic wall, muscle layers are longitudinal and arranged in bundles which usually are very thick in the parietal coelomic wall. In some species, segments show signs of differentiation. Some segments may even fuse to form specialized regions. Budding or fragmentation leads to formation of new free-living secondary cell colonies. Budding can occur at each segment. Also gametes can be produced in each segment in the visceral coelomic wall, but in some species the gamete production is restricted to few segments. Gametes are usually released into coelom for maturation and storage and then exit via metanephridial canal.

In Mollusca (Chaparro OR *et al* 2002, Eyster LS 1995, Fishera GR and Dimock RV 2002, Gibson GD 2003, Gros O *et al* 1997, Hickman CS 1995, Hohenlohe PA 2002, Kay MC and Emler RB 2002, Nielsen C 1998, 2001, Page LR 2000, Reynolds PD 2002, Ruthensteiner B *et al* 2001, Von Boletzky S 2003, Zardus JD 2002, Zardus JD and Morse MP 1998), the cleavage is spiral and the free-swimming body, a veliger, has essentially the same topology as the trochophore, but usually develops additional structures such as shells, velar lobes, and foot. It transforms without settling, forming a free-living juvenile stage which then grows and matures to become a free-living adult stage. A large area of dorsal integumental wall forms a fleshy mantle which usually expands in folds covering the body laterally and enclosing more or less spacious mantle cavity. The mantle may secrete calcareous spicules or one or more calcareous shells. The form of the shell is highly variable. The postoral area of the ventral integumental wall forms the foot. The ciliated gills, the ctenidia, are thought to be homologues of the lophophore. The gut is usually U-shaped. In the floor of the buccal cavity, the specialized gland secretes a rasp-like band of thickened, toothed chitinous cuticle, a radula. In the stomach, mineral particles move from the stomach lumen into intestine, whereas food particles move into extremely expanded diverticula for absorption and

intracellular digestion. There are two or even more pairs of coeloms and metanephridial canals which likely are rudiments of additional segments, suggesting that ancestral Mollusca were able to form secondary cell colony by internal budding but this ability became rudimentary later. Gametes are produced in the coelomic wall and usually exit via metanephridial canals into the mantle cavity.

In Nemertea (Henry JQ and Martindale MQ 1996, Jondelius U *et al* 2004, Maslakova SA *et al* 2004, Nielsen C 1998, 2001, Senz W 1997, Turbeville JM 2002), the cleavage is spiral but the gastrula rather develops into a helmet-shaped free-swimming stage of the initial body, a pilidium, sometimes with ear-flap-like lateral lobes on each side. Without to reach the trochophore stage, the pilidium immediately starts to form the secondary cell colony by internal budding, producing a long worm with a poorly established segmentation pattern. In some species, the pilidium even reaches the stage with unpaired and paired bladders which however do not develop an internal solenoid but undergo rather an aberrant development, forming the so called embryonic disks. The worm has a straight gut with a number of pairs of lateral branching diverticula. Above the mouth, there is a long tubular proboscis which may be retracted into a spacious unpaired coelom and may be everted for the capture of the prey or for defense. When everted, it may be lost and the regeneration of a new proboscis is very rapid. Branches of paired protonephridial canals are arranged serially along the worm body. The worm is extremely fragile, and usually disintegrates into fragments which then rapidly regenerate the whole worm body. In space between the integumental and gastral wall, small bladders are arranged serially along the body on either side. At maturity, these bladders swell due to gamete production. Gametes are released through tiny canals in the integumental wall.

In Platyhelminthes (D'Souza TG *et al* 2004, Hoshi M *et al* 2003, Nielsen C 1998, 2001), the cleavage is spiral and the developing initial body begins to form a trochophore and even develops a pair of protonephridial canals and a set of projecting lobes with ciliary bands at margins. But later, it enlarges axially at the expense of these lobes, which shrink and gradually disappear, and becomes a free-living body that is dorso-ventrally flattened to varying degrees and anterior-posteriorly elongated. The body has no gut, but some species develop a branched gastral cavity which may be a homologue of the digestive diverticula. The body clones itself by fission and a large population of bodies is formed. In parasitic species, the initial body is able to form secondary cell colony by adding of new segments so that a long segmented worm is formed which is extremely fragile and disintegrates into fragments. Gametes are formed in the innermost compartment of the wall within which a very complex system of specialized sacs, canals, and copulatory organs develops. The fertilization is always internal.

In Arthropoda (Akam M 2000, Guerao G *et al* 2004, Møller OS *et al* 2004, Nielsen C 2001, Olmstead AW and LeBlanc GA 2001, Vieira RRR and Rieger PJ 2004, Vogt G *et al* 2004, Zrzavy J and Stys P 1997), the initial solenoid-shaped body usually undergoes cloning by internal budding, forming a free-living secondary cell colony which is a linear series of repeating segments with a common gut. Segmentation usually manifests itself both externally and internally. However, the signs of segmentation may be eliminated during later development. Whereas all segments ancestrally were similar in structure and function, they mostly differentiate in modern species. Similar segments

are usually organized in specialized regions, the tagmata. Primitively, each segment bears a pair of appendages which are thought to be homologues of the lophophore. There is however a tendency to lose appendages from some segments. In addition to a flexible cuticle, an appendage is covered by a linear series of hard circular articles. Specialized muscles within the wall of the appendage may move the articles separately. Appendages may be frequently branched. There is a variety of specialized appendages adapted for reception, feeding, food manipulation, respiration, locomotion, and copulation. Just the ability to modify endlessly the basic appendage form is a key to the overwhelming success of Arthropoda due to the number of individual cell progression species. Each segment has a pair of small coelomic bladders associated with a pair of metanephridial canals, but most of coeloms soon obliterate or coalesce with the spacious innermost compartment of the wall which is unluckily called a haemocoel, since it is filled by blood and contains a plexus of blood canals. Only few metanephridial canals persist in marine species. In terrestrial species, the excretion occurs through tubular diverticula of the gut, the Malpighian tubules. Generally, since the cuticle hardens and must be molted to permit growth, the juvenile secondary cell colony passes through a series of intermediate stages, instars, until reaching the adult size and the ability to initiate meiosis. Gametes are produced in the wall of the few remaining coeloms and shed through their modified metanephridial canals. Fertilization may occur both externally and internally. There is a large variety of developmental patterns.

For example, in crustacean Arthropoda such as Cirripedia (Harvey R *et al* 2003, Watanabe H *et al* 2004), the hatching stage is a free-swimming nauplius which is actually a secondary cell colony. The only signs of segmentation are three pairs of appendages which are used in swimming and feeding. Subsequent molts transform the nauplius into a cypris with a bivalved mantle, the carapace, and more segments with or without appendages. The cypris swims for a week or two in the plankton and then settles with a preoral region to the substratum. It moves over the substratum using first appendages and, when it finds a suitable side, secretes an adhesive to attach itself permanently and become a sessile colony. The preoral region may form a flexible muscular stalk. The setose appendages become oriented upwards and are used to filter particulate food or capture prey. The carapace encloses the mantle cavity and the body. Within the carapace, the calcareous valves grow with the body but do not molt, whereas the rest of the exoskeleton does.

In other Arthropoda, the development may deviate greatly from ancestral pattern and contain instars differing from each other dramatically.

In Onychophora (Bartolomaeus T and Ruhberg H 1999, Mayer G *et al* 2004, Nielsen C 2001), the archenteron of the gastrula becomes compressed, but a new wide opening, called mouth-anus, soon opens in the same area. At the posterior region of the anus, a pair of compact cell bands emerges in the space between the integumental and gastral walls, grow forwards along the sides of mouth-anus, and form a row of coelomic bladders on each side. The lateral lips of mouth-anus fuse creating a solenoid-shaped body. Each coelomic bladder divides into a dorsal and ventral part. Each ventral bladder differentiates into the metanephridial canal with a thick-walled funnel and a thin-walled sacculus. Most dorsal bladders collapse and their walls become incorporated into the innermost compartments of the integumental and gastral walls. Remaining dorsal

bladders fuse and become a place of gamete production. Gametes are shed through modified metanephridial canals. The body is clearly a free-living secondary cell colony. There are numerous indices that Onychophora must be seen as a specialized, terrestrial offshoot from the early aquatic Panarthropoda.

In Tardigrada (Hohberg K and Greven H 2005, Nelson DR 2002, Nielsen C 2001, Suzuki AC 2003), the development of the primary body plan is poorly studied. The formation of a solenoid-shaped body with four pairs of coelomic bladders in space between integumental and gastral walls has been reported. But, the origin of the coelomic walls is uncertain and their fate has not been documented. The segmented body is rather a free-living secondary cell colony. Since Tardigrada retain such ancestral features as the constancy of cell number in some regions and the ability to go into cryptobiosis, they must be seen as a very early offshoot of Panarthropoda.

In Chaetognatha (Nielsen C 2001), the blastula develops the archenteron with two primordial cells situated at the bottom. They soon detach from the wall, move into the archenteron, and divide once. The antero-lateral parts of the archenteron wall form a pair of folds which grow towards the archenteron opening carrying primordial cells at the tips. The anterior part of the archenteron thus becomes divided into one median and two lateral sacs. As the archenteron opening closes, sacs become bladders. But a new opening breaks through from an anterior invagination to the median sac. The anterior parts of the lateral bladders become pinched off. The body elongates and curves, and all cavities and lumina disappear. The gastral cavity becomes flat and its wall is bordered by the lateral masses, which meet along the midline at the posterior end of the body. The newly hatched initial body is completely compact, but the gastral cavity and two pairs of coeloms soon become re-established. Whereas the anterior coelomic bladders fuse together, the posterior bladders form a median mesenterium and become quite thin-walled laterally. Finally, each posterior bladder develops a transverse fold which divides lateral part of the coelom into an anterior and a posterior cavity, each with one of the primordial cells. The anus breaks through at the level of transverse folds and the body becomes a modified solenoid-in-solenoid. The innermost compartment of the wall consists of muscles. The outermost compartment of the integumental wall is mostly a multilayered epithelium which consists of an outer layer of polygonal cells covering two or more layers of interdigitating cells. The epithelium secretes cuticle, teeth, and spines. It rests on a basement membrane which extensions form fins. The mouth opens into a pharynx, which leads to a tubular intestine and further to a short rectum. In some species, anterior part of the intestine has a pair of diverticula. The outermost compartment of the coelomic wall is a myoepithelium. Each primordial cell enters the space between the integumental and coelomic walls and gives rise to an elongate mass within which the gametogenesis occurs at the maturity: eggs in the anterior masses, sperm in posterior masses, respectively. The eggs are stored in paired canals which open at the level of the anus and function as seminal receptacle. Sperm are shed into the coelom where they mature.

In Echinodermata (Byrne M *et al* 2003, Chen BY and Chen CP 1992, Chia FS *et al* 1993, Emler RB 1995, Gosselin P and Jangoux M 1998, Hart MW 2002, Henry JJ *et al* 1991, Komatsu M *et al* 2000, Lacalli TC 2000, Lacalli TC and West JE 2000, McEdward LR and Janies DA 1997, Nakano H *et al* 2002, 2003, 2004, Nielsen C 1998,

2001, Selvakumaraswamy P and Byrne M 2000, Sumida PYG *et al* 2001, Tominaga H *et al* 2004), the blastula develops an expanded archenteron. Three pairs of coelomic bladders are pinched off from the gastral wall into the space between the integumental and gastral walls. The secondary invagination of the integumental wall fuses with the archenteron to form the gut. The early free-swimming stage, a dipleurula, later develops in any direction of specialization depending on species. The late free-swimming stage swims, but soon or later settles to bottom, and undergoes remarkable transformation, converting it into the juvenile stage. The transformation is characterized by changing of one coelomic compartment into a unique system consisting of a perioesophageal ring and five radial canals, establishing pentameric symmetry. The pentamery which in itself is secondary can be recognized in all juvenile and adult stages of Echinodermata, but the free-swimming stage is always bilateral symmetric. Among Echinodermata, Crinoidea (sea lilies and feather stars) retain the most ancestral appearance of the juvenile and adult stages: the late free-swimming stage transforms into a sessile stage that possess a stalk in sea lilies, the oral surface with a mouth at center is oriented upward, the branched arms encircle the mouth, the gut is U-shaped so that the anus is also oral but displaced to periphery. The free-swimming stages of some few species of Asteroidea (sea stars) (Bosch I *et al* 1989, Knott KE *et al* 2003, Vickery MS *et al* 2002) and Ophiuroidea (brittle stars) (Balsler EJ 1998) are known to be able to clone themselves by budding, usually from the posterior part of the body, in some cases producing feeding stages and in other cases producing pre-feeding stages that then complete early development and form feeding stages. Recently, the spontaneous cloning of free-swimming stages has been detected in Holothuroidea (sea cucumbers) and Echinoidea (sea urchins and sand dollars) too (Eaves AA and Palmer AR 2003). The cloning of free-swimming stages may be therefore an ancient ability of Echinodermata. Adult stages of Echinodermata are known to possess considerable regenerative capacities as well as the ability to clone themselves by fission or budding (Thorndyke MC *et al* 2001, Wilkie IC 2001).

In Pterobranchia (Lester SM 1988, Mayer G and Bartolomaeus T 2003, Nielsen C 2001), the elongated free-swimming stage of the initial body has two pairs of flattened bladders laterally to the gut. The lumina of these bladders are referred to as the mesocoel and metacoel. After a short period of free-swimming, the initial body starts to test the substratum creeping on the ventral side. Then, it settles with the ventral depression and secretes a thin surrounding cuticle. All organs disappear and the transformation involves the development of the sessile stage rather from a compact mass of cells. At the upper side, a collar consisting of one to nine pairs of the feather-shaped tentacles is developed. In the interior, a compact mass of cells arrange into a bladder which becomes a globular stomach and a narrow rectum. An invagination from the ventral integumental wall develops between tentacles and fuses with stomach. The new gut is U-shaped, the anus is situated a short distance behind the ring of tentacles. After a few days, the cuticle breaks open and the sessile stage starts feeding and growth. The lower side stretches into a narrow stalk. The upper side, the proboscis, becomes a flat shield with a narrow neck used in creeping and secreting the tube. In the proboscis, there is an impaired protoel which opens to the exterior through a pair of dorsal canals. A pair of collar mesocoels surrounding the pharynx send extensions into the tentacles. The mesocoels communicate with the exterior through a pair of dorsal canals which open postero-laterally. The major part of the gut is suspended in mesenteria

formed by the median walls of the paired metacoelic bladders. The metacoels extend into the stalk region where the septum between them can be lacking. Thus, three main regions of the wall, the integumental wall, gastral wall, and coelomic wall, may be clearly distinguished. The innermost compartment of the wall contains muscle layers and a plexus of blood canals and lacunae. One blood canal near the protocoel has specialized cells, podocytes, and is believed to be a site for filtration of primary urine. The outermost compartment of the wall is a monolayered myoepithelium. A dorsal extension of the pharynx, a stomochord, runs anteriorly between the pharynx and protocoel. The stomochord consists of vacuolated cells and is either compact or has a lumen. The pharynx has a pair of gill slits. The tube material contains keratin and collagen. The secondary cell colony is sometimes quite extensive aggregations of tubes housing solitary sessile stages with lively cloning themselves by budding. However, the bodies are not completely sessile. They can move around in the tubes and may even leave the aggregation and start to build a new one if conditions become too hostile. Gametes develop within the metacoelic wall. They are shed directly into the exterior through short canals. Fertilized eggs are usually deposited in the tubes where the early development takes place.

In Enteropneusta (Cameron CB 2002a, 2002b, Nezlin LP and Yushin VV 2004, Nielsen C 1998, 2001, Ruppert EE *et al* 1999, Tagawa K *et al* 2001, Urata M and Yamaguchi M 2004), the early free-swimming stage, a tornaria, has unpaired protocoelic bladder and paired mesocoelic and metacoelic bladders which origin varies between species. The tornaria usually swims for several months, increasing in size, but whether it can clone itself has not been reported. The innermost compartment of the wall becomes spacious and is filled by a gelatinous matrix. In full-grown tornaria, the wall of the buccal cavity forms a narrow dorsal invagination, a stomochord. The pharynx develops two or three pairs of gill pockets. At transformation, the pharynx extremely stretches anterior-posteriorly so that the hindgut becomes pulled backwards. The gill pockets become situated in the anterior part of the metacoelic region of the body where the gill slits break through. Additional gill slits develop in a series behind the first few. The newly formed gill slits are oval, but soon become U-shaped due to the development of a dorsal outgrowth, the tongue bar. The number of gill slits increases with growth to near 200 in some species. Each slit opens laterally into an atrium which in turn opens to the exterior via the pore so that two rows of pores are seen on the dorsal integumental wall. The metacoelic wall finally grows around the atria and forms the musculature. The strengthened basement membrane develops between the cell layers. The oesophageal wall forms folds restricting the lumen. Posterior to the oesophagus, the gut forms numerous paired diverticula within which the phagocytosis and intracellular digestion occurs. The anus is terminal. The protocoelic wall develops a thick layers of muscles so that the most anterior part of the body becomes an almost spherical to elongate conical proboscis. There is a small canal connecting the protocoel with the exterior. One of the blood canals within the protocoelic wall contains podocytes. The proboscis is supported by the strengthened basement membrane of the dorsal buccal wall and stomochord. A pair of canals connects paired mesocoel with the exterior, opening in invaginations of the integumental wall which develop in association with the atria of the first gills. Dorsal to buccal cavity, the integumental wall develops an unpaired bladder, a collar cord, by regular infolding in some species or through delamination in others. The lumen of the collar cord usually obliterates partly or completely, and persists in a few species

only. Lateral to each row of atria, a row of small bladders develops in space between the integumental and metacoelic walls, forming rounded ridges or flat wings. At maturity, these bladders swell due to the gamete production and bulge into the metacoel. Gametes are shed through tiny canals in the integumental wall. Fertilization usually occurs externally.

In Tunicata (Urochordata) (Chadwick-Furman NE and Weissman IL 2003, Jeffery WR and Swalla BJ 1992, Lacalli TC 1999, Manni L *et al* 2004, McHenry MJ and Patek SN 2004, Nielsen C 2001, Satoh N 1994, Tarjuelo I and Turon X 2004, Young CM and Vazquez E 1995), the gastrula has an elongated archenteron. A longitudinal strip of the gastral wall then becomes internalized. Some cells of this strip interdigitate to form a median row of disk-shaped cells, a urochord, which becomes surrounded by a basement membrane. Near the urochord, a strip of the integumental wall folds forming an elongated neural cavity which expands encompassing the opening of the archenteron. Then, the longitudinal lips of the neural cavity gradually fuse together so that a neuro-gastral lumen becomes internalized. The body begins to curve, the neural lumen separates from the gastral one and elongates. The body now consists of a globular trunk and a slim tail which becomes very pronounced and encircles the trunk. The rather voluminous gut may have a lumen, but has neither mouth nor anus. The anterior part of the neural tube becomes divided longitudinally with the left part separated from the main neural tube. Three frontal adhesive papillae are the attachment organs used in settling. They contain sensory and secretory cells. Just behind the adhesive papillae, a shallow dorsal invagination develops into an oral siphon. In the pharynx, a ventral longitudinal groove develops into an endostyle. Pair of integumental invaginations fuses dorsally forming an atrium with a median anal siphon. Between the atrium and pharynx, two or three gill openings break through on each side. The tail contains the posterior part of the main neural tube, the urochord, and two lateral bands of muscle cells which are arranged in 2 or 4 rows. The posterior part of the neural tube becomes a spinal cord consisting of four longitudinal rows of cells innervating muscle cells. The urochord becomes a stack of coin-shaped cells and is surrounded by a strengthened basement membrane. A matrix lenses secreted between urochordal cells fuse into a central rod. The urochordal cells become more and more flat and arrange into the monolayered bladder with a rod in the lumen. The only trace of the original gut is a row of cells along the ventral side of the urochord. The tail wall secretes a thin tunic with a cellulose-like tunicin. The tadpole-like body hatches, swims for a short period, then settles and transforms into a barrel-shaped sessile stage of the initial body. At settling, the body attaches by adhesive papillae, the cuticle is shed, and the tail becomes retracted. The cellular material of the tail and of the main neural tube becomes resorbed. The separate left part of the neural tube persists and becomes a cerebral ganglion. The gut rotates so that the oral siphon finally points away from the substratum. In the innermost compartment of the wall, primordial cells secrete a semi-fluid matrix and the body swells. The pharynx expands into a spacious branchial basket with a high number of gill slits. The water is sucked in through the mouth which forms an incurrent siphon. The food particles are caught by a fine mucous filter net secreted continuously by the cells of the endostyle and transported to the oesophagus. The filtered water passes through gill slits into the both lateral atria and out through middorsal excurrent siphon. A narrow oesophagus leads into a stomach with various digestive diverticula and glands. An intestine opens in the left atrium. Extensions from the endostyle can form two epicardial



bladders with more or less expanded lumina which are interpreted as a mesocoel. There is a plexus of blood canals and lacunae surrounded by basement membrane without cellular covering. Only around a large lacuna situated ventral to the posterior part of the pharynx, cells arrange into a pericardial chamber which develops into a heart with circular musculature. The heartbeat and the direction of blood flow reverse periodically. Blood canals traverse the pharyngeal wall between the gill slits. In blood, primordial cells, usually called haemoblasts, give rise to all blood cells such as lymphocytes, leukocytes, vacuolated cells, pigment cells, and nephrocytes. Nephrocytes accumulate waste products and transport them to the special regions of the tunic. The thick tunic is secreted by integumental wall which sends extensions with blood canals in it. The budding can take place not only in the sessile stage but also precociously in the free-swimming stage. The buds develop through a large number of different types. The budding usually gives rise to the growing secondary cell colony. Also special dormant stages contribute to distribution of the individual cell progression in space. In secondary cell colony, bodies of three consecutive generations are connected to each other by a stalk and have a common plexus of blood canals. Circulating haemoblasts can undergo meiosis and the developing eggs move through plexus of blood canals from older to younger bodies as they grow and mature. Some circulating haemoblasts can concentrate in the interior of any bodies. They usually form one or more compact cell masses in space between the integumental and atrial walls on either side. When the cell mass receives an egg derived from the preceding generation, part of this cell mass differentiates into an egg envelop, forming an egg follicle and a follicle stalk, whereas the remainder differentiates to produce sperm. When the cell mass receives no egg, it differentiates as a whole to produce sperm. Gametes are usually shed from the atrial siphons. The fertilization and the rapid development usually take place in seawater, but sometimes also in special brood chambers situated in the atrium.

In Cephalochordata (Gemballa S *et al* 2003, Holland LZ 2002, Holland PWH 2000, Nielsen C 2001), the gastrula elongates during the archenteron formation. The archenteron opening narrows, the dorsal side of the gastrula becomes flattened, the dorso-median gastral wall thickens, and the overlaying integumental wall forms the so called neural plate which becomes overgrown by a pair of lateral folds. Posteriorly these folds continue around the archenteron opening. The folds soon fuse leaving an anterior opening so that the neuro-gastral canal is formed. However, a neural cord with a narrow cavity, a neurocoel, soon separates from the archenteron. One medio-dorsal longitudinal plate of the archenteron wall folds up forming the notochord, and two lateral longitudinal plates form grooves within which the segmentation begins. Each groove breaks up into a row of bladders which are the first signs of the secondary body plan. The bladders differentiate first at the anterior end, and new bladders become added anterior-posteriorly. The developing anterior bladders have a lumen which arises as a small diverticulum in open connection with the archenteron, while the following bladders are more compact. By the time two pair of bladders have formed, the body hatches and swims by movement of cilia, continuing the formation and differentiation of bladders. At the stage of about 7-8 pairs, the left anterior diverticulum remains small but the right becomes larger so that the bladders at the right side become situated a little more posteriorly than those of the left side and the bladders of the two sides alternate. Each bladder divides into a dorsal and ventral bladder. Whereas dorsal bladders, a somites, retain separate lumina, the ventral bladders soon fuse to a pair of longitudinal

bladders which in turn fuse together to one coelomic bladder surrounding the gut except mid-dorsally. The median part of each somite becomes a thick muscular wall which extends dorsally around the neural bladder and ventrally around the coelomic bladder, giving rise to the myomere of that body segment. Another part of the somite remains a thin wall which lateral portion attaches to the integumental wall, forming with the muscular wall a cavity called a myocoel, and medial portion develops extension with a sclerocoel, separating the muscular wall from the notochord. At the stage of about 17 somites, an invagination forms on the left side of the anterior integumental wall and fuses with the archenteron wall. Just behind the newly formed mouth, the pre-oral pit, a pit of Hatschek, is formed. At the same time, the first gill slit breaks through on the right side near the ventral midline well behind the mouth. Additional gill slits develop in a series behind the first fill slit. This series slowly moves to the left side, while a new series of gill slits develops on the right side. The gill slits soon become U-shaped by the development of tongue bars. Each vertical slit becomes divided into a row of gill pores by the development of transverse synapticles. The system becomes supported by a skeleton formed by a thickened basement membrane. The gill slits divide the coelom into a number of narrow spaces. Much later, a pair of longitudinal dorso-lateral integumental folds grow outward above the gill slits, flex downward covering the branchial basket, and finally fuse at the ventral midline leaving only a posterior atrial opening, some distance in front of the anus, creating thus the atrium. These folds contain coelomic compartments which are originally parts of the coelom. The cilia of the gill pores create the water current which enter the spacious pharynx through the large mouth and buccal cavity, passes through the gill pores to the atrium and leaves through the atrial opening. The mouth is surrounded by a ring of slender tentacle-like cirri. The buccal cavity has a series of ciliated grooves making up the so called wheel organ. The buccal cavity is separated from the pharynx by a transverse muscular velum with an aperture of adjustable diameter in the center. Along the pharynx, there is a ciliated ventral endostyle, producing mucus with iodine, and a dorsal groove. Captured food particles are transported posteriorly to the oesophagus and then to the intestine with an anterior digestive diverticulum and a short rectum. A row of nephridial canals is found on each side in the branchial region. Each canal opens in the atrium at the base of the tongue bar. The nephridium is a cell of unique art, the cyrtopodocyte, consisting of one part forming a usual podocytic lining of a blood canal and another part which resembles a protonephridial solenocyte. At the dorsal region of the body, there is a longitudinal series of small bladders know as a fin boxes. The septa between adjacent boxes represent the fin rays. The neural cord is surrounded by a cells arranged in sheath. The notochord is composed of large, vacuolated, disk-like myoepitheliocytes arranged in a stiff longitudinal column which is surrounded by a thick sheath of cells. In space between the integumental and atrial walls, there are two mid-lateral rows of small bladders. At maturity, these bladders swell due to the gamete production and bulge into the atrium. There is a male-female dimorphism. Gametes are shed into the atrium through ruptures. Fertilization usually occurs externally.

In Vertebrata (Gilbert SF 2000, Shimeld SM and Holland PWH 2000), the ontogenesis is usually complicated through large amounts of yolk or by species-specific extraembryonic structures so that the stages of the primary and secondary body plan formation are hard to discern. The ontogenesis resembles that of Cephalochordata, but has many important differences. The neurocoel of Cephalochordata is not closed and is

actually a dorsal atrium with an anterior opening. On the contrary, the neurocoel of Vertebrata is closed and just the anterior portion of the neural bladder becomes the brain. The spacious ventral atrium of Cephalochordata is completely developed and connects with pharyngeal lumen through gill slits. On the contrary, the ventral atrium of Vertebrata is vestigial and presented merely by a pair of narrow posterior ducts. The lateral portions of the integumental wall do not contribute to the formation of the ventral atrium as in Cephalochordata but develop into the so called neural crest and placodes. Just the neural crest and placodes contribute to the formation of many structures considered to be novelties of Vertebrata, including the branchial skeleton, cranium, and numerous cranial ganglia.

When the secondary body plan of Vertebrata is established, the wall generally involves:

- poorly segmented integumental wall,
- poorly segmented gastral wall arranged as a common gut,
- segmented chordal wall arranged as a chain of compact chordal bladders,
- poorly segmented atrial wall arranged as a pair of atrial ducts,
- poorly segmented neural wall arranged as an elongated neural bladder,
- poorly segmented coelomic wall arranged as a coelomic bladder,
- poorly segmented meningeal wall arranged as a meningeal bladder,
- segmented somitic wall arranged as paired chains of compact somitic bladders,
- segmented germinal wall arranged as paired chains of compact germinal bladders.

Generally, Vertebrata display the most sophisticated spatio-temporal organization of the wall. In some Vertebrata, the wall integrity is maintained by complex interactions between asymmetric cell progressions of different types.

## **Conclusions**

The present-day biosphere is merely a tiny slice from the general cell progression, a visible top of iceberg in ocean of time. However, although the number of individual cell progressions in this tiny slice represents only a small fraction of the whole, it is enormous. Much work is needed to describe and systematize this diversity completely.

The evolution of individual cell progressions intrinsically involves the evolution of cells which phylogenetic diversity in biosphere can be summarized in a compact system of cell types.

The spatio-temporal organization of individual cell progressions is much more variable than that of cells. Therefore, it is not surprisingly that the diversity of individual cell progression types is enormous. This diversity depends greatly on the phylogenetic cell type. Above, the diversity of individual cell progressions was reviewed with special focus on formation of cell associations. Therefore, more attention was paid to phylogenetic cell types by which the formation of cell association takes place during the life history of individual cell progressions.

Animal individual cells progressions were reviewed in more details. To describe the formation of animal cell associations, a notion of a closed and orientable surface was used. In contrast to abstract mathematical surface, the real biological surface is made up not by dimensionless points but by three-dimensional matrix with embedded cells. So, it is actually a closed and orientable wall, since there is a distance between its two sides. The thickness of the wall may have regional differences in magnitude. Additionally, the two sides of the wall can be differently designated according to their orientation to interior or exterior of the cell association. To avoid confusion, one must be aware that the wall is not a boundary of the cell association but just its body.

The complexity of animal cell association enhances gradually at different phylogenetic and ontogenetic stages. Vertebrata display the most sophisticated spatio-temporal organization of the wall.

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## **How cell associations construct themselves**

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