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## Evolution, phylogeny and classification of Suctorea (Ciliophora)

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### Summary

The monograph is concerned with suctorian ciliates. Using the materials collected and generalizing all literary data available, the author has proposed original hypotheses of suctorians' origin and the main regularities of the evolution of the taxa. A new scheme of phylogeny of Suctorea has also been elaborated. Based on this research a new system of the class Suctorea, including 4 subclasses, 15 orders, 2 suborders, 41 families and 124 genera, has been proposed.

Key words: Suctorea, evolution, phylogeny, classification

### Introduction

This monograph is concerned with suctorian ciliates. This group is one of the most species-rich (531 according to our data) groups among Ciliophora Doflein, 1901. Suctorian species constitute about 7% of ciliate species that have been described to date.

**Habitats.** Suctorians can be found in all types of water bodies on a wide diversity of hosts and substrates. The majority of these ciliates are commensals of various water invertebrates or vertebrates (fishes or turtles). Suctorian ciliates also inhabit the intestine of horses, rhinoceroses, guinea pigs and elephants (Timoshenko, 1996; Van Hoven et al., 1998, and others).

There are both ectoparasitic and endoparasitic species among suctorians. These ciliates often parasitize on other ciliates including suctorians. The parasites of multicellular organisms such as rotifers, molluscs, sabellid polychaetes, turbellarians are also known.

Several podophryid and trichophryid suctorian

species are planktonic. Typically they are freshwater forms but marine species (the genus *Marinecta* Jankowski, 1978) have also been recorded. It seems likely that all representatives of this ecological group are secondarily planktonic.

**Morphology.** Suctorian ciliates are largely sessile forms. The adult stage (trophont) is usually the stalked zooid (Fig. 1). The unstalked flattened (Fig. 2) or ramified forms are less common. The presence of one or more tentacles, as a rule with a distal extension (knob) is most characteristic of the group.

The ciliature is lacking in trophonts of suctorians (except the commensals of guinea pigs). Only in the ventral zone near the contractile vacuole canal a small field of barren kinetosomes with reduced ectoplasmic fibrils may occur (Seravin and Gerassimova, 1978).

The body of suctorian trophonts characteristically ranges in size from 100  $\mu\text{m}$  to 200  $\mu\text{m}$  but certain ophryodendrid suctorians may be as large as 800  $\mu\text{m}$ ,



Fig. 1. *Discophrya elongata* (Claparede et Lachmann, 1859) from the leg of water bug *Ranatra linearis* (Linnaeus, 1758). Scanning electron microscopy (x1200). Abbreviations: *tn* – tentacle; *z* – zooid; *st* – stalk.

while *Dendrosoma radians* Ehrenberg, 1838 reaches 2000  $\mu\text{m}$  (Dovgal, 1996) or even 5000  $\mu\text{m}$  (Batisse, 1994).

The body shape of suctorian trophonts is widely diversified, which has been associated with sessile mode of life, substrate diversity, environment factors and lack of cilia (Batisse, 1994), with the substitution of the cytostome (a characteristic centre responsible for ciliate shape) by numerous tentacles (Dovgal, 1996). Interestingly, coloniality is presumably not characteristic of suctorian ciliates.

Exoskeleton is present as different stalks and loricas. Besides lorica, completely covering the ciliate body, semilorica or basotheca, covering only the lower part of the body is often observed. The stylothea (thecostyle) represents type of loricas. The organisms with stylothea adhere to the substrate by means of their stalk-like protuberance. The mucous lorica forming at the expense of the glycocalyx development is not uncommon in Suctorea as well.

There is invariably one macronucleus in suctorians. The macronucleus varies in shape from spherical or oval (in small species) to ribbon-like or branched (in large species). The micronuclei are generally numerous in suctorian ciliates and unevenly distributed around the macronucleus or (rarely) within the depressions in the latter.

There are contractile vacuoles in suctorians of all ecological groups: freshwater, marine and parasitic. The number of contractile vacuoles can vary in accordance with suctorian species, age and size. For example, there are mainly one or two vacuoles in exogemmin and endogemmin suctorians, whereas numerous vacuoles

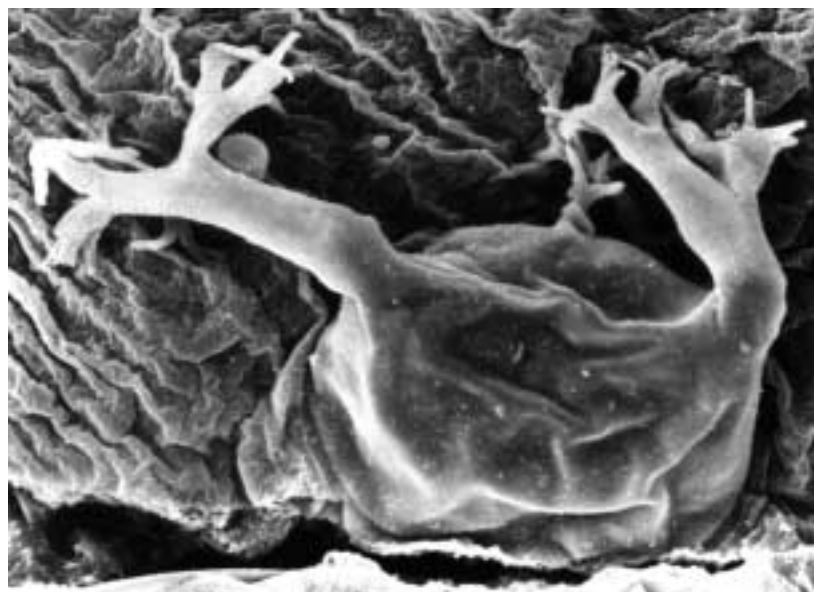


Fig. 2. *Dendrocometes paradoxus* (Stein, 1851) from the gill of gammarid amphipod *Gammarus lacustris* Sars, 1863. Scanning electron microscopy (x860).

(up to several tens in *Discophrya ochthebii* Matthes, 1954) may occur in inversogemmin suctorians.

**Life cycle and development.** Just like other sessile ciliates suctorians as a rule reproduce by different modes of budding. Their life cycle consists of a free-swimming larval stage (swarmer) that (except vermigemmins) possesses locomotor ciliature. The morphology of suctorian swimmers is less diverse than that of trophonts. Still attempts at their classification have been made (Guilcher, 1948a, 1951; Batisse, 1994).

The reproduction by monotomy is retained in parapodophryans, parasitic sphaerophryans, phalacrocleptid suctorians as well as in intestine inhabitants. Certain parasitic species (for example, *Sphaerophrya parameciorum* Maupas, 1881) reproduce by both monotomy and budding (Jankowski, 1963).

In some tokophryid suctorians trophotomy or reactive budding may occur under adverse conditions. In the course of trophotomy the entire trophont generates locomotor ciliature and then breaks away from the stalk. However, it is strictly speaking not reproduction, as it does not result in an increase in the number of individuals.

The swarmer attaches to a substrate suitable for settlement. Shortly after settling, it undergoes metamorphosis involving resorption of the ciliature and development of the stalk, lorica (if present) and tentacles from the tentacle anlagen (Bardele, 1970; Dovgal, 2002).

The modes of suctorian reproduction hold much systematic significance and will be discussed below.

**Feeding.** Suctorian ciliates capture and devour their prey by tentacles. No less than 10 hypotheses of the functioning of suctorian tentacles can be enumerated (Hertwig, 1875; Plate, 1886; Eismond, 1891; Collin, 1912; Penard, 1920a; Kahl, 1931; Kormos, 1938a; Kitching, 1952; Hull, 1961; Bardele, 1972, etc.). A full consideration of most of them is contained in M. Canella's (1957) monograph, many of the hypotheses being mainly of historical interest.

Suctorian ciliates exhibit a certain selectivity as regards food objects (Canella, 1957). Free-swimming ciliates are the basic prey of suctorians. Capture of flagellates and amoebae has also been observed on some occasions.

**The origin of the group.** The origin of the suctorians has been discussed by many authors. The hypothesis of the origin of the suctorians from rhynchodids is most widely accepted at present (Batisse, 1994). However, as shown below, the above mentioned proposals cannot be reconciled with some morphological features of suctorians.

**Systematic problems.** There are several versions of the suctorian classification which differ essentially in

taxonomic rank of the group, numbers of subordinate taxa, etc. (Jankowski, 1978, 1980, 1981; Matthes et al., 1988; Batisse, 1994; Dovgal, 1996).

There are two main approaches to the derivation of the Suctorea system.

D. Matthes and his followers believe that the classification should be elaborated on the basis of non-adaptive characters. Naturally, the adoption of such a limited group of characters hampers the development of a rational classification. Furthermore, the problem of non-adaptive nature of morphological characters is ambiguous. This seems to be the reason why D. Matthes did not necessarily use the principles proclaimed in regard to suctorians. In particular, the shape of macronucleus was not used in suctorian taxonomy (Matthes et al., 1988).

Another approach to construction of the Suctorea classification was stated by A.V. Jankowski (1978, 1980, 1981). This author has proceeded from the assumption that if the organisms differ from the characteristics of their group only by one sufficient character they must be classified in separate taxon. Only presence or absence of a character may be used as a basic guideline for classification, and not the degree of character distinction.

Several other versions of the Suctorea classification (Corliss, 1979; Dovgal, 1996, etc.) might be considered as compromise settlements. However, the recent classification of A. Batisse (1994) is worth special consideration. The author has proposed to discriminate three suctorian orders that differ by the mode of budding. For representatives of the order Podophryida Jankowski, 1973 exogemmy without any invaginations ("heteromorphic division") is characteristic. The order Exotropida Batisse, 1994 includes the forms with exogemmy that starts with invagination of the cortex (mainly ephelotins and ophryodendrids). Finally, internal budding of the representatives of Entotropida Batisse, 1994 begins with invagination. As a result, the suctorians with both ciliary and non-ciliated swimmers fall into Exotropida and those with internal and external budding (parapodophryans, thecacinetins, etc.), into Entotropida. This classification constitutes a radical departure from A.V. Jankowski's, D. Matthes' and our views on Suctorea classification.

The versions of suctorian classification by A.V. Jankowski (1980), D. Matthes with co-authors (1988) and A. Batisse are summarised below.

#### **Classification of A.V. Jankowski (1980):**

- Class Suctoria Claparede et Lachmann, 1858
- Subclass 1. Tomogenea Jankowski, 1978
- Order 1. Podophryida Jankowski, 1967

- Order 2. Metacinetida Jankowski, 1978
- Order 3. Paracinetida Jankowski, 1978
- Order 4. Urnulida Jankowski, 1978
- Order 5. Allantosomatida Jankowski, 1978
- Order 6. Ophryocephalida Jankowski, 1978
- Order 7. Tachyblastonida Jankowski, 1978
- Subclass 2. Vermigenea Jankowski, 1978
  - Order 1. Spelaeophryida Jankowski, 1978
  - Order 2. Dendrosomidida Jankowski, 1978
  - Order 3. Thecacinetida Batisse, 1975
  - Order 4. Ophryodendrida Jankowski, 1975
    - Suborder 1. Asteriferina Jankowski, 1978
    - Suborder 2. Stylostomatina Jankowski, 1978
    - Suborder 3. Ophryodendrina Jankowski, 1975
- Subclass 3. Endogenea Collin, 1912
  - Order 1. Acinetida Raabe, 1964
    - Suborder 1. Tokophryina Jankowski, 1978
    - Suborder 2. Acinetina Raabe, 1964
  - Order 2. Trichophryida Jankowski, 1978
  - Order 3. Dendrosomatida Jankowski, 1975
    - Suborder 1. Dendrosomatina Jankowski, 1978
    - Suborder 2. Stylophryina Jankowski, 1978
  - Order 4. Pseudogemmida Jankowski, 1978
  - Order 5. Endosphaeriida Jankowski, 1978
- Subclass 4. Evaginogenea Jankowski, 1978
  - Order 1. Discophryida Jankowski, 1975
  - Order 2. Dendrocometida Raabe, 1964
- Subclass 5. Neotenea Jankowski, 1978
  - Order 1. Cyathodiniida Jankowski, 1978
- Suctorina incertae sedis
  - Order 1. Phalacrocleptida Jankowski, 1978

**Classification of D. Matthes and others (1988):**

- Order Suctorina
  - Suborder Endogenea Collin, 1912
    - Family Tokophryidae Jankowski, 1978
    - Family Acinetidae Stein, 1859
    - Family Acinetopsidae Jankowski, 1978
  - Suborder Evaginogenea Jankowski, 1978
    - Family Discophryidae Collin, 1912
  - Suborder Exogenea Collin, 1912
    - Family Podophryidae Bütschli, 1889
    - Family Metacinetidae Bütschli, 1889
    - Family Ephelotidae Kent, 1880
    - Family Tachyblastonidae Grell, 1970
    - Family Thecacinetidae Matthes, 1956
    - Family Spelaeophryidae Batisse, 1975
    - Family Ophryodendridae Stein, 1867

**Classification of A. Batisse (1994):**

- Subclass Suctorina Claparede et Lachmann, 1858
  - Order Podophryida Jankowski, 1973

- Suborder Podophryina Jankowski, 1973
  - Family Podophryidae Haeckel, 1866
  - Family Paracinetidae Jankowski, 1978
  - Family Severonidae Jankowski, 1981
  - Family Phalacrocleptidae Kozloff, 1966
- Suborder Metacinetina Jankowski, 1978
  - Family Metacinetidae Bütschli, 1889
  - Family Urnulidae Fraipont, 1878
- Order Exotropida Batisse, 1994
  - Suborder Ephelotina Raabe, 1964
    - Family Ephelotidae Kent, 1880
  - Suborder Ophryodendrina Batisse, 1975
    - Family Rhabdophryidae Jankowski, 1970
    - Family Stylostomatidae Batisse, 1975
    - Family Lecanophryidae Jankowski, 1973
    - Family Ophryodendridae Stein, 1867
    - Family Spelaeophryidae Batisse, 1975
- Order Entotropida Batisse, 1994
  - Suborder Thecacinetina Batisse, 1975
    - Family Thecacinetidae Matthes, 1956
    - Family Corynophryidae Jankowski, 1981
    - Family Parapodophryidae Jankowski, 1973
    - Family Tachybalstonidae Grell, 1950
    - Family Allantosomatidae Jankowski, 1978
  - Suborder Acinetina Raabe, 1964
    - Family Acinetidae Stein, 1859
    - Family Tokophryidae Jankowski, 1978
    - Family Trichophryidae Fraipont, 1878
    - Family Endosphaeriidae Jankowski, 1978
  - Suborder Dendrocometina Raabe, 1964
    - Family Dendrocometidae Haeckel, 1866
    - Family Stylocometidae Jankowski, 1978
  - Suborder Discophryina Batisse, 1975
    - Family Discophryidae Collin, 1912
    - Family Cyathodiniidae da Cunha, 1914

It can be seen that suctorians remain a relatively poorly known taxon. For example, in our estimation about 100 suctorian species have not been observed since their discovery. There is no consensus of opinion among ciliatologists regarding the origin, taxonomical rank and position of this group within Ciliophora. Currently the data on phylogenetical reconstructions in the taxon are practically not used in discussions concerning suctorian systematics.

This paper reviews 20 years of the author's investigations on suctorians. Using the materials collected during that time and generalizing all literary data available, the author has proposed original hypotheses of suctorian origin and the main regularities of the taxa evolution. The new scheme of phylogeny of Suctorea has been elaborated. On the basis of this research the classification of Suctorea has been revised.

## CHAPTER 1. THE ORIGIN OF SUCTORIAN CILIATES AND THE TAXONOMIC POSITION OF THE GROUP

**The advancement of concepts of the origin of suctorians**

The feeding by tentacles of a characteristic morphology has always been believed to be the most characteristic feature of suctorians. Correspondingly, the search for the origin of the group was reduced to establishing the origin of this organelle by the majority of authors.

Early investigators believed that suctorians had affinity with heliozoans. In particular, R. Sand (1899) argued that the tentacles of suctorians were homologous to the axopodians of heliozoans. In contrast, other authors (Ehrenberg, 1838; Dujardin, 1841; Claparede and Lachmann, 1859, 1861; Hertwig, 1875; Fraipont, 1877, 1878; Plate, 1888) believed that the tentacles were novel organelles, characteristic of Suctoria alone.

It was also conjectured (Gegenbaur, 1870, cited after Canella, 1957; Hickson, 1903) that the suctorian tentacles were homologous to the cilia of ciliated protozoans and were derived from the cilia by means of «progressive differentiation». This concept was for some time supported even with the results of electron microscopy. M. Rudzinska and K.R. Porter (1953) detected the nine microfibrilles surrounding the tentacle axonema in *Tokophrya infusionum* (Stein, 1859). In the authors' opinion, the correspondence of the number of fibrilles in the tentacle to the number of doublets of microtubules in a cilium testifies to a common origin of these organelles.

It was the opinion of O. Bütschli's (1889) that suctorian tentacles were derived from the cytostome of carnivorous mobile ciliates by means of its special rearrangement. At first, a sole tentacle originated as an adaptation to the feeding by suction of prey, then the polymerization of the "mouth opening" took place.

B. Collin (1912) has supplemented the Bütschlian hypothesis, suggesting that the necessity to consume the prey that is predator-size or even larger was the reason of the origin the tentacles. B. Collin also discussed the possible simultaneous origin of several tentacles from the cytopharynx of peritrichs and supposed that suctorian tentacles might be novel formations that have originated concurrently with regression of the cytostome.

Of prime importance was the description of rhynchodid ciliates by L. Plate (1888). This author found two species from the genus *Hypocoma* Gruber, 1884 (named *Acinetoides* by L. Plate) that are parasites of marine ciliates. In L. Plate's opinion hypocomes

are an intermediate link between suctorians and other ciliates because they have both somatic ciliature and tentacles and reproduce by binary fission and not by budding.

O. Bütschli (1889) believed that this affinity was possible. In contrast, R. Sand (1899) reasoned that *Hypocoma* was not an intermediate form but the result of adaptation to parasitism. B. Collin (1912) anticipated that Hypocomidae Bütschli, 1889 were derived from the ephelotid suctorians by means of neoteny.

E. Chatton and A. Lwoff (1939) grouped hypocomes with some related forms in the order Rhynchodida Chatton et Lwoff, 1939. It was E. Chatton's and A. Lwoff's opinion that whereas infraciliature of rhynchodids involved bipolar kineties, apolar or circumpolar kineties were characteristic of suctorians. Assumptions of the affinity between suctorians and rhynchodids were for some time rejected.

F. Stein (1867) was the first who paid attention to the similarity between the hunting tentacles of some hymenostomates and suctorian tentacles. C. Mereschkowsky (1882, 1883) believed that the carnivorous planktonic tentaculate hymenostomates from the genus *Mesodinium* Stein, 1862 are intermediate between Suctoria and other ciliates. In J. Entz's (1883) opinion suctorians undoubtedly derived from ciliates of the genus *Actinobolina* Strand, 1926 (named *Actinobolus* Stein, 1867). Further still, this author reasoned that *Actinobolina* was a possible suctorian swarmer. O. Bütschli (1889) also did not rule out some affinity between *Actinobolina*, *Mesodinium* and Suctoria.

Although A. Kahl (1934) took into consideration unquestionable likeness between the tentacles of hypocomid and suctorian ciliates, yet he eliminated Hypocomidae as the possible ancestors of Suctoria. A. Kahl (1931) believed that suctorian tentacles derived not from the cytostome but from the hunting tentacles of Prostomata Schewiakoff, 1896. He conceived that the tentacles of *Mesodinium*, *Actinobolina*, other tentaculate Prostomata and suctorian tentacles are «amazingly similar in appearance». The ciliate which is the most similar to suctoreans is *Legendrea belle-rophon* Penard, 1914. In A. Kahl's view *Dactylochlamys pisciformis* Lauterborn, 1901 is similar to the swarmers of suctorian ciliate *Parapodophrya soliformis* (Lauterborn, 1901) (see Fig. 19, A) to the point where it might be confused with them.

In A. Kahl's view, the tentacles of suctorians represent the final result of evolution process, which traces back to the origin of trichocysts in ectoplasm of

*Pseudoprorodon* Blochmann, 1886. The phylogenetic lineage of tentaculous Ciliophora (Spathidiidae Kahl, 1929 and Didiniidae Poche, 1913) has originated from the species of *Pseudoprorodon* devoid of trichocysts. Some *Pseudoprorodon* species with trichocysts in turn the ancestor of actinobolin ciliates on the one hand, and, on the other hand, of *Dactylochlamys* Lauterborn, 1901, *Enchelyomorpha* Kahl, 1930<sup>1</sup>, *Peitiada mirabilis* Frenzel, 1892 and the most primitive suctorians – *Parapodophrya* Kahl, 1931.

Kahl's concept had been rather popular before the electron microscopic investigations disclosed that there was no likeness in morphology of suctorian and actinobolin tentacles (Holt and Corliss, 1973).

Owing to application of the advanced silver impregnation technique I. Guilcher (1947, 1948a, 1948b, 1950a, 1950b, 1951) established the bipolarity of suctorian kineties. Based on this evidence it was concluded (Faure-Fremiet and Guilcher, 1947) that there was no longer any barrier for considering rhynchodids and suctorians as relatives. The suctorians were transferred into Holotricha Stein, 1859 as a result (Corliss, 1964; Raabe, 1964).

Thus the majority of specialists reverted to the idea of rhynchodids as possible ancestors of suctorians. It has taken place despite the fact that I. Guilcher (1951) agreed with Chatton's and Lwoff's (1949) opinion that there was no point in discussing a possible homology between suctorian and rhynchodid tentacles in the absence of information about functioning of these organelles and their formation during ontogeny.

A.V. Jankowski (1978) has believed that not podophryids are most primitive suctorians (as might be expected) but ephelotids and discophryids, their swarmer ciliature pattern being similar to rhynchodid ciliature. He also proposed (Jankowski, 1980) to combine rhynchodids and suctorians in the superclass Rhynchosuctorida Jankowski, 1980.

In the new revised system of Ciliophora (Puytorac, de, et al., 1993) both rhynchodid and suctorian ciliates are classified in the class Phyllopharyngea de Puytorac et al., 1974 in the subphylum Epiplasmata de Puytorac et al., 1993 as the subclasses Rhynchodia Chatton et Lwoff, 1939 and Suctorina correspondingly. The systematic position is in agreement with the tradition to consider the two groups as related.

In our opinion it is profitable to consider the tentacles of suctorians and rhynchodids both in respect both to morphology and the functioning of these organelles. It is also interesting to discuss the feeding organelles of representatives of several other carnivorous protists.

## The morphology and functioning of feeding organelles of suctorians and some other carnivorous and parasitic protists

A typical suctorian tentacle is a cylindrical cell protuberance furnished with a distal bulge (knob). The tentacles are usually 1–2  $\mu\text{m}$  thick but their length may exceed 100  $\mu\text{m}$  (Bardele, 1974). Early investigators mentioned the «inner canal» of tentacle by which the suction of prey proceeded.

M. Rudzinska (1965) has discovered that the «canal» (axonema) consists of a pattern of microtubules. The number of microtubules may vary in different species of Suctorina. There are, for example, 49 microtubules in *Tokophrya infusionum* (Rudzinska, 1965), 56 in *Acineta tuberosa* Ehrenberg, 1834 (Bardele and Grell, 1967) and from 200 to 400 in *Ephelota gemmipara* (Hertwig, 1875), *Dendrocometes paradoxus* Stein, 1851 and *Choanophrya infundibulifera* (Hartog, 1881) (Batisse, 1966; Bardele, 1972; Hitchen and Butler, 1973). However the general arrangement of microtubules remains the same and is unique among feeding structures of the ciliates (Lynn and Foissner, 1994).

The suctorian tentacle has two layers of microfibrilles in axonema (Fig. 3, A). The outer layer is cylindrical and formed from microtubules that are separated from each other. The inner layer is arranged in several arm-bearing microtubular ribbons or folds that slightly overlap.

The cylindrical part of tentacle is covered with an envelope. The envelope is an extension of the cell cortex and includes cellular and alveolar membranes, glycocalyx and epiplasm.

In the knob (under perilemma) several short extrusomes named haptocysts are spaced (Rudzinska, 1965; Bardele and Grell, 1967; Batisse, 1967, 1994). Haptocysts are similar to toxicysts and are considered as a variety of the latter (Hausmann, 1978).

The suctorial tube (tentacle) of rhynchodids is also a cell protuberance with a distal knob (Fig. 3, B, C). The knob is coated with a membrane containing numerous pores (Lom and Kozloff, 1968; Puytorac, de, 1994)<sup>2</sup>. There is an axonema consisting of one microtubular layer. The microtubules are arranged in such a manner that they form several pleats (Fig 3, D). The axonema penetrates deep into cell body. The extrusomes of Rhynchodia (trichocysts or haptotrichocysts) are located near the base of the tentacle. Their ejection has never been observed and their function remains a mystery (Puytorac, de, 1994).

<sup>1</sup> *Enchelyomorpha* is in fact a suctorian ciliate (Foissner et al., 1995; Foissner and Foissner, 1995).

<sup>2</sup> It is likely that these are not true pores but this needs further investigations.

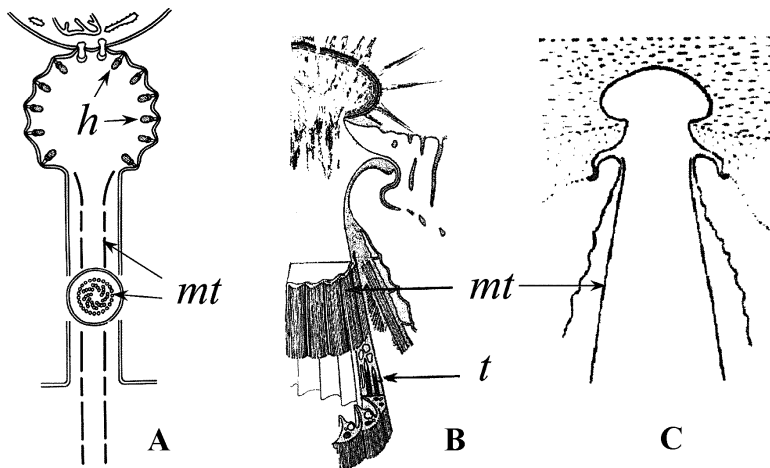


Fig. 3. The structure (schematic drawing) of the tentacles of suctorian (A, according to Bardele, 1972) and rhynchodid ciliates (B and C, according to Lom and Kozloff, 1968). Abbreviations: *mt* – microtubules; *t* – trichocysts; *h* – haptocysts.

Consequently, distinct similarities between the morphology of suctorian and rhynchodid tentacles are in existence. At the same time, there are several differences that should be considered. For example, the axonema of the rhynchodid suctorial tube contains only one microtubular layer and the knob lacks extrusomes.

M. Rudzinska (1965) was the pioneer investigator who proposed the idea of the important role of microtubules in suctorian feeding (at the expense of peristaltic microwaves of the microtubules). However, C. Bardele's (1972, 1974) proposals are widely accepted to date.

This author considered the tentacle of *D. paradoxus* as a model and attached much importance to interactions between the microtubules of the tentacle and the membrane of prey.

C. Bardele (1974) believed that the distal end of suctorian tentacle functions like the cytostome of gymnostome ciliates. The feeding process in Suctoria begins from the invagination of the knob membrane with the prey's cytoplasm inward the tentacle due to a motion of projections found on several microtubules of the inner layer in the distal end of the tentacle (Fig. 4, B). The outer layer of microtubules appears to act as a bearing structure.

In I. Lom's and E. Kozloff's (1968) view, the rhynchodids, alternatively, feed by osmosis through the pores in the knob of suctorial tube. A more recent publication (Puytorac, de, 1994) has to do with external digestion. Thus, the structure of suctorial tube in rhynchodids precludes the feeding of the type characteristic of carnivorous ciliates include carnivorous suctorians. The knob is submerged into a host tissue (gill filaments, hepatopancreas) or cell body. Living rhynchodids have been observed to change their localization freely (Bower and Meyer, 1993). Thus, the microtubular axonema in rhynchodid tentacle is probably acting as a bearing structure only.

Consequently, the tentacles in suctorian and rhynchodid ciliates operate in a distinctly different manner.

On the contrary, there is much more similarity in morphology and function between feeding organelles of suctorian ciliates and several unrelated carnivorous protists.

M. Canella (1957) has given several examples of protists that feed in the same manner as suctorians. He has mentioned *Bodo* sp. and one marine dinoflagellate species. In fact, the phagotrophic dinoflagellate

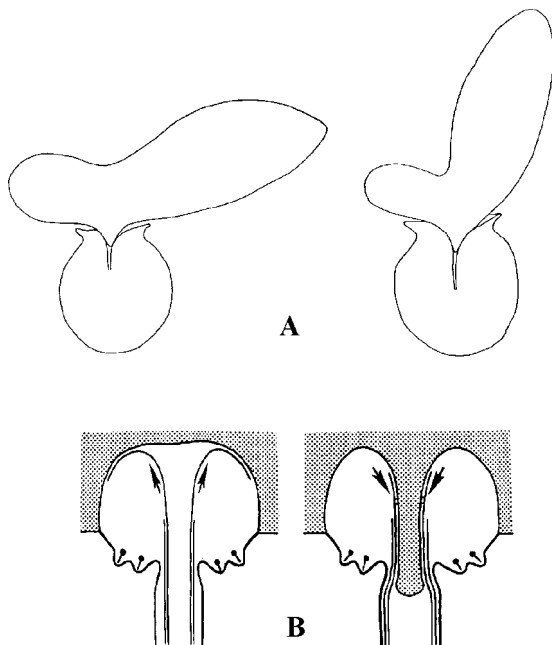


Fig. 4. The initial phases (schematic drawing) of prey ingestion in *Didinium nasutum* Müller, 1786 (A, after Wessenberg and Antipa, 1970) and suctorians (B, after Bardele, 1972).



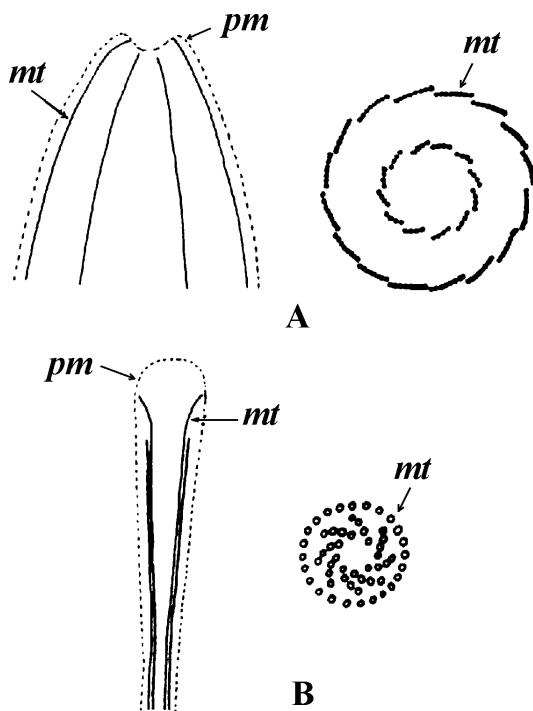


Fig. 5. The schematic drawing of the katablepharid conoid (A, according to Mylnikov et al., 1998) and suctorian tentacle (B, according to Lee et al., 1991). Abbreviations: *mt* – microtubules; *pm* – plasma membrane.

*Gymnodinium fungiforme* Anissimova, 1926 ingests prey cytoplasm through a highly extensible organelle named peduncle and analogous to the tentacle of suctorian ciliates (Spero, 1982).

A.P. Mylnikov et al. (1998) have indicated that the feeding mechanism of carnivorous katablepharid flagellates closely parallels that of suctorians. The feeding apparatus in katablepharids likewise contains two microtubular layers (Fig. 5). In this connection it should be noted that katablepharid flagellates are possible ancestors of ciliates (Lee et al., 1991). It was therefore speculated that the system of cortical alveoli in ciliates and *Katablepharis* spp. is similar (Lee and Kurgens, 1992). In fact this is undeniably a case of convergence (Patterson, 1994).

### The origin and systematic position of suctorian ciliates (the author's concept)

In our opinion the question how the free-living carnivorous suctorian ciliates could have derived from specialised parasites of ciliates of mollusc mantle complex such as *Rhynchodia* is still open. The opposite lineage – from preying to parasitism – seems more likely to us.

It is highly probable that the quest for structures, homologous to the suctorian tentacle is more promising

in mobile ciliates that feed on the predator-size prey than in forms (such as rhynchodids, cyrtophorins, etc.) with specialized tentacle-like organelles.

*Didinium nasutum* (Müller, 1786) is one of the species best studied in this respect (Wessenberg and Antipa, 1970) and may serve as a model.

Prey organisms suitable for *Didinium* Stein, 1867 are ciliates, flagellates, amoebae and even turbellarians. The feeding apparatus of *Didinium* consists of cell protuberance (proboscis or rostrum) (Fig. 6) furnished with two types of extrusomes – long trichocysts and short toxicysts (pexicysts). Along the length of the proboscis runs the nemadesma. In addition there are cortical ribbons of microtubules and a fibrous ring. On the basis of movements of these fibrillar structures the proboscis is retracted and screwed in the cell body together with prey (Fig. 4, A).

We believe that the mechanism of prey ingestion by *Didinium* is close to that in the suctorian tentacle, since the rostrum contractile structures operate similarly to the inner microtubular layer of the tentacle (Fig. 4, A, B). The nemadesma of proboscis also involves microtubules (Holt, 1972) and resembles the axonema of the tentacle whereas pexicysts may be homologous to haptocysts.

For the conversion from swallowing of large prey to more economic suction only a functional substitution of the nemadesmal fibrilles was probably necessary. It is likely that in a certain mobile ciliate with the ingestion mechanism similar to that of *Didinium* the outer part of microfibrilles was no longer contractile but began to work as a bearing structure. The inner part of microfibrilles retained contractility. As a result, the structure might have started functioning like katablepharid conoid or dinoflagellate peduncle.

The intensification of the function of prey capturing possibly proceeded by means of the elongation of the organelle plus the polymerization and accumulation of the extrusomes. The latter process, in turn required the increasing of the surface of the organelle tip and decreasing of the number of extrusomes. In such a manner the knob of the tentacle and haptocysts were possibly developed.

The progressive evolution of protists is associated with the increase of body size. Such increase may cause a drop in the effectiveness of cell organelles or organelle systems functioning. This drop might be avoided either by the increase of organelle size or by the organelle number multiplication. The second way (polymerisation) has been used by protists much more often, as noted already by V.A. Dogiel (1951).

Thus there is a good probability that the tentacle has originated even in planktonic ancestors of Suctoria, but polymerization of the feeding organelles was

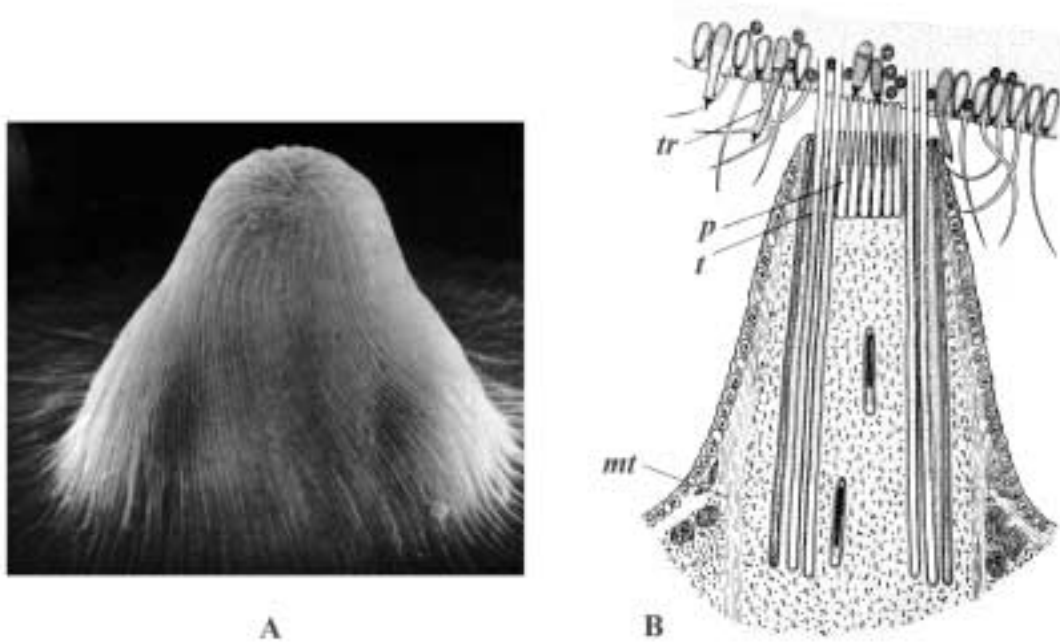


Fig. 6. The structure of the proboscis of *Didinium nasutum* Müller, 1786 (according to Wessenberg and Antipa, 1970). A – the general view (SEM); B – structure (schematic drawing). Abbreviations: *mt* – microtubules; *t* – trichocysts; *p* – pexicysts; *tr* – prey trichocysts.

associated with the transition to the sessile mode of life (Bardele, 1974; Dovgal, 2000).

In the recent version of the phylum Ciliophora system (Puytorac, de, et al., 1993) didiniids are relegated in subphylum Filicorticata de Puytorac et al., 1993, class Litostomatea Small et Lynn, 1981, order Spathidiida Foissner et Foissner, 1988 as the suborder Didiniina Jankowski, 1978.

The predominance both of ectoplasmic and endoplasmic filaments for the forming of cortex is characteristic for all Filicorticata representatives. The somatic ciliature is of the same type and consists of monokinetes. Oral cilia may be absent, but their infraciliature is built up both by monokinetes and dikinetes. These kineties are formed during ontogenesis by involvement of the anterior parts of somatic kineties (telokinetal stomatogenesis). The prevailing view today is that the possession of dikinetes is an ancestral characteristic (Eisler and Fleury, 1995). In this case, somatic monokinetes are secondary in filicorticates.

In addition, the reduction of somatic ciliature up to one or two transversal kineties is characteristic for didiniids. There are three types of extrusomes: mucocysts, trichocysts and pexicysts.

As already noted, both suctorians and rhynchodids reside in the subphylum Epiplasmata. It is the opinion of P. de Puytorac's et al. (1993) that the presence of both somatic and oral dikinetes and monokinetes with

kinetodesmal fibrilles is characteristic for all representatives of the subphylum. The reduction of trophont ciliature are characteristic of suctorians and sphaenophryid rhynchodids. In the general case the ciliature consists of two main ciliary fields except for Suctorina swimmers that have only one main field of cilia. A well-developed epiplasm under the alveolar layer is characteristic of Ciliostomatophora de Puytorac et al., 1993 too. Stomatogeneses are telokinetal, parakinetal and apokinetal. For all taxa of the superclass Ciliostomatophora a specialised microtubular skeleton (cytopharynx) surrounding the phagoplasm is characteristic. It is believed that in suctorians an identical structure is present as the axonema of the tentacle (Batisse, 1994). The presence of the subkinetal microtubules in the cortex is a common feature of ciliostomatophores.

As evidenced by the above, several suctorian characteristics such as the pattern of the swimmer ciliature or the analogue of cytopharynx slightly deflect from the features common for the superclass or at least for the class Phyllopharyngea.

Ciliature is developed in swimmers of Suctorina only (except cyathodiniids). The trophonts invariably (except *Phalacrocleptes* Kozloff, 1966) bear kinetosomes close to the pore of the contractile vacuole or form an anarchic field on the apical surface of the cell body.

There are additional microfilaments in the cortex of several suctorian species. For example, there may be interrupted (*Heliophrya* De Saedeleer et Tellier, 1930, *Trichophrya* Claparede et Lachmann, 1859) or continuous (*Dendrocometes* Stein, 1851, *Cyclophrya* Gonnert, 1935, *Allantosoma* Gassovsky, 1918) layers of microtubules acting as bearing structures. There are additional microtubules near the stalk in *Tokophrya* Bütschli, 1889 or in the actinophore of *Loricodendron hollandei* (Batisse, 1969) (Sundermann and Paulin, 1981, Batisse, 1994). Several structures that closely resemble each other are observed in *Stylocometes* Stein, 1876 (Maccagno, 1934), *Stylostoma* Milne, 1886 and *Asterifer* Jankowski, 1967 (Collin, 1912; Guilcher, 1950b). However, no subkinetal microtubules or barren basal bodies were found in swimmers of *Enchelyomorpha* (Foissner and Foissner, 1995).

At the same time, some structures of the cortex are similar in didiniids and suctorians. It should be noted that existing differences between the groups (essential at first glance) refer to the composition of the cortex.

In the diagnoses of ciliate subphyla, however, we deal with the predominance of different types of microfilaments. In particular, there is epiplasm in all ciliates, but it is weakly developed in the taxa that are outside Epiplasmata.

In our opinion the provision of suctorian cortex with subkinetal microtubules is a more distinctive property, which hampers the idea on the affinity between didiniids and suctorians. It should be mentioned that as a result of small-subunit rDNA investigations *Didinium* and suctorian species were found in separate (though adjacent) clades (Riley and Katz, 2001). However, the possibility, even if unlikely,

of the origin of suctorians from some ancestor common with didiniids can not be ruled out.

Nonetheless, the origin of suctorians from mobile carnivorous ciliates that feed in the same manner as didiniids is highly plausible.

Consequently, the podophryid suctorians that retained the capacity for binary fission and a simple mode of symmetry may be thought of as the most primitive group of these ciliates. The podophryid shape of the cell body may be probably considered as initial for suctorians.

As discussed above, Suctoria are classified in the class Phyllopharyngea (Pyutorac, de, et al., 1993; Pyutorac, de, 1994) as a subclass. In the context of our hypothesis on the origin of the group the position of Suctoria in the same taxon as Rhynchodia and Chonotrichia Wallengren, 1895 appears artificial. However, the presence of subkinetal microtubules in suctorian cortex may suggest the affinity between Suctoria and other representatives of Phyllopharyngea.

In our opinion some way out would be found if the group is left in the superclass Ciliostomatophora with the rank of the class Suctorea Claparede et Lachmann, 1858.

As a result the system of the subphylum takes the following form:

- Subphylum Epiplasmata de Puytorac et al., 1993
- Superclass Ciliostomatophora de Puytorac et al., 1993
- Class Phyllopharyngea de Puytorac et al., 1974
- Class Suctorea Claparede et Lachmann, 1858
- Superclass Membranellophora Jankowski, 1975
- Class Nassophorea Small et Lynn, 1985
- Class Oligohymenophorea de Puytorac et al., 1974

## CHAPTER 2. SOME REGULARITIES IN THE EVOLUTION OF SUCTOREA

The development of the mode of budding is most frequently considered as a basic tendency in suctorian evolution (Collin, 1912; Kormos and Kormos, 1957; Kormos, 1959, etc.). Rarely the tendency to the body branching was also discussed (Jankowski, 1972). The type of budding ignored by the latter author in the work mentioned.

In our opinion the development of Suctorea was associated with their transition to the obligate sessile mode of life, i.e., with occupation of the hydrodynamic boundary layer as an adaptive zone (Dovgal, 2000).

Similar to other sessile protists, the structures affording the interaction with environment have evolved in suctorians (Dovgal, 2000). The idea about the evolution of mainly cortical structures in ciliates (Puytorac, de, et al., 1993; Eisler and Fleury, 1995) is

probably close to the above viewpoint. The protection of protomit from environmental influence is a fundamental tendency in evolution of suctorian reproduction.

### The evolution of budding

In almost all taxa of sessile ciliates (including Suctorea) the transition from binary fission (monotony) to budding can be followed. In the case of the loss of motility the transition to irregular fission with formation of migratory stage was beneficial. It gave additional benefits since the parental individual did not require transformation. Thus it remained active and retained its localization, which was important in conditions of topical competition (Dovgal, 2000).

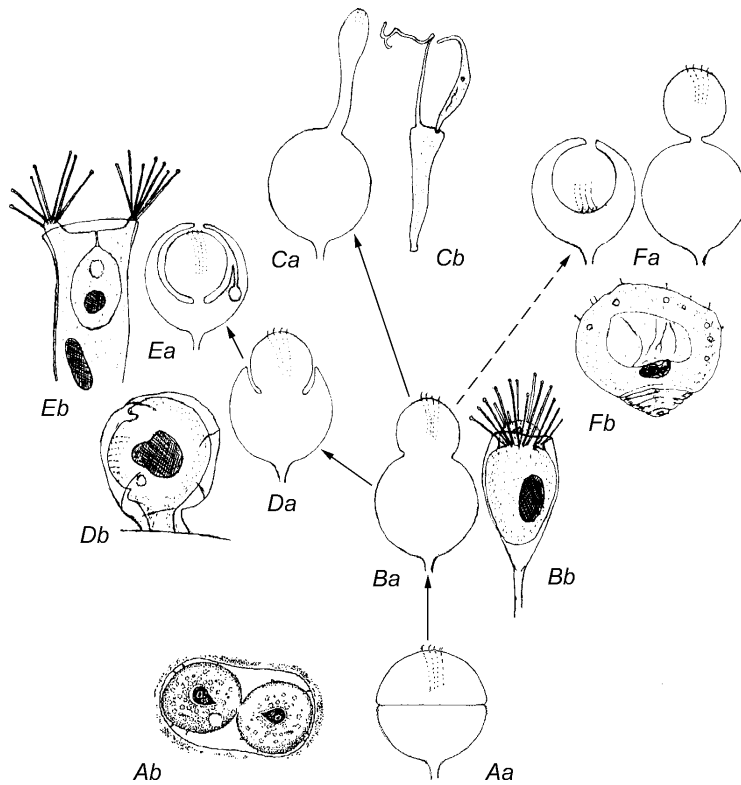


Fig. 7. Hypothetical diagram of the evolution of reproduction modes in Suctorea (according to Dovgal, 1996, modif.). Aa — binary fission (Ab — division of *Sphaerophrya parameciorum* Maupas, 1881, according to Jankowski, 1963); Ba — exogemmic budding (Bb — budding of *Paracineteta livadiana* Merschowsky, 1881); Ca — vermigemmy (Cb — budding of *Ophryodendron prenanti* Duboscq, 1925, according to Kahl, 1934); Da — semi-circumvaginative budding (Db — reproduction of *Pseudogemmides globosa* Kormos, 1935); Ea — endogemmic budding (Eb — reproduction of *Acineteta nitocrae* Dovgal, 1984); Fa — inversogemmy (Fb — budding of *Discophrya lichtensteinii* Claparede et Lachmann, 1859).

Binary fission is retained in podophryid suctorians such as *Parapodophrya* or parasitic *Sphaerophrya* Claparede et Lachmann, 1859 (Fig. 7, Ab). *Phalacrocleptes*, the parasite of sabellids and allantosomids, inhabitants of the intestine of the horses, elephants and rhinoceroses reproduce only by monotomy (Fig. 8).

Ephelotids, metacinetids, paracinetids, etc. reproduce by exogemmic budding. There are several modes of exogemmy that are characterized by the

number of forming buds (monogemmy or polygemmy) as well as by the bud position on the parental cell.

For example, for marine paracinetid and ephelotid suctorians the apical position of bud is characteristic.

In contrast, in the freshwater metacinetids the tomit is generated laterally on the trophont body. The parasitic suctorians from the genus *Manuelophrya* Matthes, 1988 and some relative genera reproduce in a similar manner.

One further characteristic feature of budding in the suctorians is the generation of tomit in the partial invagination of trophont cortex (semi-circumvaginative budding). As a result the swarmer in the invagination is probably more protected.

For the group of marine (with several exceptions) suctorians that mainly live on the harpacticoid copepods (Fernandez-Leborans and Tato-Porto, 2000) a distinctive type of budding called vermigemmy is characteristic. The swarmers of these suctorians are devoid of ciliature. These swarmers perform the function of dispersion, crawling onto the new hosts over the surfaces of the copulating copepods (Dovgal and Kochin, 1997). There is a special larval adhesive organelle (sucker) for this purpose. Vermigemmy is characteristic of *Ophryodendron* (Claparede et Lachmann, 1859), *Lecanophrya* (Kahl, 1934), *Rhabdophrya* (Chatton et Collin, 1910) and some others.

For most suctorian species endogenous budding is characteristic. This mode of budding starts with an invagination of a part of the cortex (Bardele, 1970). This

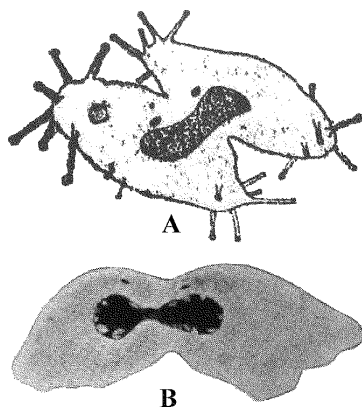


Fig. 8. The reproduction of (A) *Allantosoma intestinalis* Gassowski, 1918 (according to Strelkow, 1939) and (B) *Phalacrocleptes verruciformis* Kozloff, 1966 (according to Kozloff, 1966).

cortical region bears several basal bodies (the generative area). Next the brood pouch with the swarmer anlage is formed in the mother cell. Both monogemmy and polygemmy are characteristic too. The acinetids, trichophryids, endosphaeriids, etc. reproduce in this manner.

Finally, inversogemmy is characteristic of several genera (*Discophrya*, *Dendrocometes*, etc.) that are mainly commensals of freshwater insects and crustaceans.

During inversogemmy a deep invagination of the cortex (the brood pouch) is generated by means of its allometric growth. Next the ciliature of the swarmer develops on the pouch surface. After that the invaginated cortical fragment rapidly evaginates and is filled by a fragment of parental cytoplasm with the daughter nuclei. Finally the swarmer generated breaks away from the mother cell.

Evolutionary lineages can be modelled at least for exogemmy, vermigemmy and endogemmy.

For example, exogemmy can be easily deduced from monotomy. In podophryid suctorians that retained several modes of budding the swarmer derives the tentacles and kinetosomes for locomotor ciliature from the parental organism.

Further development of reproduction probably went in the direction of tomit protection against external exposure.

The budding area might have become displaced under the lorica (i.e. to the side of the trophont body) in loricate forms. At least a partial inversion of the protomit in a parental cell has possibly taken place in connection with the limitation of space. In this way the ancestors of freshwater metacinetid suctorians and marine paracinetids could have passed over to semi-circumvaginative budding. The latter mode of reproduction is commonly considered as intermediate between exogemmy and endogemmy (Kormos and Kormos, 1957).

In our opinion there is a good probability that in case of metacinetids this mode of budding represents no more than an evolutionary tendency. In the great majority of suctorians that reproduce by endogemmy the budding area is associated with apical rather than lateral body surface. It seems likely that possible ancestors of endogemmin suctorians should be searched among unloricate taxa. In suctorians devoid of lorica the protection of protomit can be achieved by its direct inversion into the trophont body. The progressing of the tendency probably ultimately gave rise to endogemmy.

As for vermigemmy, this mode of reproduction could have developed in connection with suctorians living on water arthropods. As this took place, the problem of

regular moult of the hosts was the most essential for the symbionts. In all likelihood, a certain span of feeding time is required for the commensal before proceeding to reproduction. The swarmers of suctorians do not feed, while the food reserve that have derived from parental cell is probably sufficient for distribution and metamorphosis only. Filter feeders such as peritrichous ciliates can begin to feed almost immediately after attachment. In contrast, carnivorous suctorians must capture the prey, resulting in additional time before the start of the budding. The arthropod larval stages often moult and are unfit for settlement by suctorians.

For example, the absence of suctorians on the naupliar or copepodit stages of harpacticoid copepods while the mature individuals serve as hosts for many suctorian species is probably associated with this factor. On the contrary, larval stages of copepods are very often infected by peritrichous ciliates.

On the contrary, the adult harpacticoids do not moult. This renders harpacticoid copepods most useful as suctorian hosts. As a result a wide variety of suctorian species are specific commensals of different harpacticoid species.

As this takes place, the ciliates are exposed to a complex of hydrodynamic factors (Dovgal and Kochin, 1995, 1997). Under these conditions, the swimming of suctorian swarmers in the immediate vicinity of host surface involves difficulties and the transition to crawling appears more beneficial. However, it was concerned with the reduction of swarmer ciliature and advent of larval adhesive structures. In this manner vermigemmy has been developed.

Inversogemmy is characteristic of only freshwater suctorians. As with vermigemmin suctorians, the host-specific species of inversogemmins inhabit exclusively the adults of invertebrates. For example, the majority of discophryid suctorians live on the imago of beetles and bugs. This suggests that the problem of the host moult is essential for these suctorians too.

It is possible that inversogemmy developed in the early exogemmins in connection with inhabiting the mobile hosts. This has aggravated the problem of protomit protection. As with other cases of «internal» budding, the submerging of protomit into the parental cell was the first step.

As an intermediate variant between exogemmy and inversogemmy the reproduction of dendrocometid suctorians may be discussed. The budding of *Dendrocometes paradoxus* starts with a deep invagination of the cortex and the brood pouch develops as a result. Next the budding that is similar to exogemmy occurs at the brood pouch bottom (Batisse, 1975).

All modes of asexual reproduction listed have formed independently but the ways in which suctorian

ciliates transited to the internal tomit formation remain an open question.

### The evolution of adhesive organelles

While giving to protists certain benefits, attachment subjects them to the problems of a counteraction to specific hydrodynamic loads. This specificity is determined by the location of sessile protists within the hydrodynamic boundary layer limits. Our investigation of some species of Suctorea (Dovgal and Kochin, 1995, 1997) has shown that their variability depends on the distribution of hydrodynamic loads in different sites of the boundary layer. We arrived at the idea that the boundary layer has a determinate spatial structure; the conditions are different in different parts of this layer.

Shear stress, hydrodynamic velocity pressure (integrated force) and other hydrodynamic loads should be mentioned as the most important abiotic factors influencing organisms in a boundary layer. Ubiquitous factors such as temperature, concentration of oxygen, dissolved organic matter, etc. are essential too. The action of all these factors is different in various parts of boundary layer, being conditioned by the spatial structure of the layer (Dovgal, 1998, 2000). The boundary layer represents a complex of potential habitats for protists. On this basis we have formulated the concept of fluid boundary layer as an adaptive zone for these organisms (Dovgal and Kochin, 1995, 1997; Dovgal, 2000).

In our opinion the development of suctorian ciliates also proceeds during the process of adaptation to the conditions in different parts of boundary layer. Examples of adaptations abound in Suctorea. In particular, the modes of attachment of suctorian ciliates to the substrates are extremely diverse.

Several suctorian species (for example, *Trichophrya*) attach to the substrate by the basal part of the body or by the stalk-like cell protuberance. However, the adhesion by means of a tectinous stalk is the most usual.

Two types of lorica are the derivatives of stalk in Suctorea. The tectinous lorica of stalked suctorians is formed by means of allometric grows of the stalk. Semilorica or basotheca, covering only the lower part of the body, belongs to this type. Stylothea (thecostyle) represents another type. The suctorians with this lorica adhere to the substrate by means of basal part of stylothea or by their stalk-like protuberance. The zooid adheres to the lorica near the apical aperture.

It is interesting to note that in several families of Suctorea (for example, Periacinetidae Jankowski, 1978) all types of lorica (include mucous one) are present.

A high degree of morphological diversity of the connection between stalk and body is characteristic of

stalked suctorians. Different basal discs and physones protect this area apart from the above mentioned lorica and basotheca. In *Tokophrya actinostyla* Collin, 1912 and *Choanophrya infundibulifera* there are several distinctive invaginations of cortex in the zone of junction between stalk and body. These invaginations are filled with tectin (Batisse, 1994) and are analogous to the endostyle of chonotrich ciliates (Dovgal, 1998). There is also a characteristic structure (papilla) in zone of junction between stalk and lorica in several loricate species such as *Paracineta patula* (Claparede et Lachmann, 1861) and *Acineta compressa* Claparede et Lachmann, 1859. A particularly complex structure (a frilled collar-like disc) is generated between stalk and body in *Tokophrya ornata* Gajewskaja, 1933 living on gammarid crustaceans from Lake Baikal.

There is an interesting adhesive organelle (similar to the cinctum of several peritrichous ciliates) in two representatives of genus *Erastophrya* Faure-Fremiet, 1943. These suctorians grip the peritrich body by two cell extensions (in *E. chattoni* Faure-Fremiet, 1943; Fig. 27, D) or a single one (in *E. wuchangensis* Chen, 1964; Fig. 27, E).

In the suctorians of the genus *Spongiarcon* Jankowski, 1981 (Fig. 23, B) living in the canals and oscula of sponges both stalk and body protuberances are present, with the unique polymerization of the stalk (Jankowski, 1981).

Several suctorian species have lost stalks in transition to the planktonic (*Sphaerophrya*, *Mucophrya pelagica* Gajewskaja, 1928) or parasitic (*Sphaerophrya*, *Pseudogemma* Collin, 1912, *Pottsiocles* Corliss, 1960, *Phalacrocleptes*) modes of life. In these cases the function of temporary (in planktonic species) or permanent (in parasitic species) attachment was transferred to ordinary or modified tentacles.

Apart from permanent adhesive organelles there are also temporary structures for attachment in swimmers of several suctorian species such as the above mentioned sucker in vermigemmins and the perforatorium in parasitic suctorians of the genus *Endosphaera* Engelmann, 1876.

A variety of attaching modes in suctorians can be considered as adaptation to different hydrodynamic loads (Dovgal and Kochin, 1995; Dovgal, 1998), which has already been discussed. In our opinion this allows us to consider the evolution of organelles as the process of adaptation to hydrodynamic factors.

Obviously the first problem for the ancestors of sessile suctorian ciliates was that of attachment to a substrate. They were subjected to action of shear stress that effects upon the base of an attached organism. Under these conditions various secretory organelles (for example, scopuloid in Suctorea) have appeared.

Besides the secretion of sticky substances secretion the increase of contact area with a substrate is necessary for a counteraction to shear stress. Hence, forms with an extended body base gained selective advantage.

The particularity of this stage was that attached organisms were located within the limits of the diffusal boundary layer where only molecular diffusion was possible. An uprise above this layer moves the animals into the area of much faster convection diffusion and gives suctorians essential benefits in feeding. In this connection some forms evolved adaptations to raising their body above the substrate. They formed stalks and the function of rising the zooid over the substrate was added to that of attachment. However, this uprise has subjected the organisms to an additional load of the hydrodynamic velocity pressure (integrated force).

During adaptation to the latter the greatest number of structures were generated in suctorians. The value of a hydrodynamic velocity pressure increases together with the body rise over substrate (Dovgal and Kochin, 1997) as well as with an increase of the body diameter (Silvester and Sleigh, 1985). The latter is especially important for sessile protists. For them the tendency to the progressive increase of body size is characteristic. For example, among suctorians the most primitive podophryids have the cell size up to 50 µm, acinetids up to 150 µm, ephelotids and stalked discophryids up to 300 µm. Accordingly the action of an integrated force should sharply increase in the zone of junction between stalk and body. Therefore practically all adaptations to this factor are aimed at strengthening this junction. Several specialized structures are formed by means of of apical allometric growth of stalk. Some types of loricas probably also generated in the same way (Dovgal, 1998).

It is necessary to mention that not all suctorians evolved structures for rising the body above the substrate. The counteraction to shear stress requires the enlargement of the base of cell body. The amplification of this function in some groups mostly went by means of formation of flattened body and increase of the body size in order to increase the area of its contact with the substrate. In the area of a conventional diffusion only feeding organelles were mounted. In such a way the characteristic outlines of heliophryid and trichophryid suctorians were probably generated. It might be well to point out that most of these forms (for example, heliophryid suctorians) have wide tectinous adhesive discs and are probably derived from the stalked ancestors.

It is our opinion that body protuberances represent the adaptations to the complex set of hydrodynamic conditions (Dovgal, 1998). The cell protuberances and stalk polymerisation in *Spongiarcon variabilis* Jan-

kowski, 1981 (Fig. 23, B) is an extreme case of such adaptations.

A set of conditions of similar character is formed around the stalks of sessile ciliates that are often used as substrates by suctorians. The most extreme hydrodynamic conditions are probably associated with inhabiting fishes. There are several ways to increase the strength of adhesion (Dovgal, 1998), but only two of them were realized by Suctorea.

One way is the symmetric allometrical growth of twin protuberances of the basis of the body. Probably in such a way the cinctum of *Erastophrya chattoni* was generated (Fig. 9, A).

The second way is unilateral allometrical growth of the body protuberance resulting in formation of a bend. A closed ring could gradually be formed at the expense of such a bend. In this way the cinctum in *Erastophrya wuchangensis* (Fig. 9, B) might have been generated. In our opinion the ingenious way of its formation gives grounds to introduction of a special term "hemicinctum" for this adhesive structure.

On the whole, the evolution of the adhesive structures in Suctorea followed the pattern usual for sessile ciliates: 1) facultative attachment (thymotaxis); 2) secretion of sticky substances; 3) increase of the attachment area; 4) rise of the body above the substrate with the formation of the adhesive organelles (stalks); 5) formation of structures protecting the zone of stalk and body connection (Dovgal, 1998).

The representatives of various suctorian taxa (with different modes of budding) have independently populated habitats with similar conditions. Analogous adhesive structures have developed in unrelated groups of these ciliates as a result.

### The evolution of the feeding apparatus

As discussed above, the suctorian tentacle is probably derived from the feeding apparatus of a certain mobile ciliate that had the ingestion mechanism similar to that of *Didinium*.

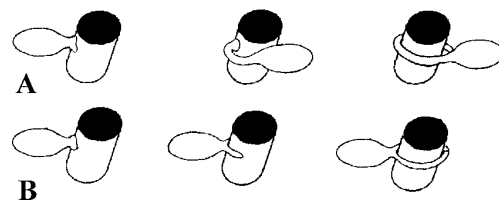


Fig. 9. Schematic drawing of possible ways of the adhesive rings formation in suctorian ciliates (according to Dovgal, 1998, modif.). A – formation of the cinctum in *Erastophrya wuchangensis*, Chen, 1964; B – formation of the hemicinctum in *E. chattoni* Faure-Fremiet, 1944.

The suctorian tentacles are widely diversified. A.V. Jankowski (1981) recognizes up to 15 types of the tentacles.

Clavate tentacles (with distal widening or knob) are the most widespread. Clavate tentacles with flared base are characteristic of representatives of *Parapodophrya*, *Lecanophrya* (Fig. 21, J) and *Lecanophryella* Dovgal, 1985 (Fig. 21, K). The tentacles of parasitic suctorians such as *Urnulla* Cl., Lachm., 1861 (Fig. 19, K), *Rhynchophrya* Collin 1909 (Fig. 28, I), *Rhyncheta* Zenker, 1866 (Fig. 25, J), etc. are extremely long and agile. The rod-like tentacles are widely distributed in ophryodendrid, pseudogemmid and some other suctorian ciliates. Finally, branched tentacles are characteristic of *Shyzactinia* Jankowski, 1981 (Fig. 23, A), *Dendrocometes* (Fig. 29, E) and some genera related to the latter.

Both rod-like and branched tentacles differ from other types of tentacles in their distal end morphology. Unlike clavate tentacles, there is a very thick layer of endoplasm in these tentacles that are uncontractile as a result (Bardele, 1972).

There are several other variations concerning tentacle structure. For example, *Slitarcon laevis* (Dons, 1918) (Fig. 24, G) in different authors' opinion has lost tentacles (Curds, 1985a) or its tentacles are very short and probably devoid of axonema (Jankowski, 1986).

The tentacles of allantosome suctorians that live in intestine of horses are short, clavate and with an axonema that is star-shaped in cross section (Sundermann and Paulin, 1981). In commensals of guinea-pig intestine (Cyathodiniidae da Cunha, 1914) the tentacles (endosprits or chilostyles) are very reduced, but with an ordinary shaped axonema and a single haptocyst (Paulin and Corliss, 1969).

There is only one haptocyst also in the tentacle of ectoparasite of sabellid polychaetes *Phalacrocleptes verruciformis* Kozloff, 1966, but its axonema is reduced down to a single layer (Lom and Kozloff, 1967). It is possible that the tentacles of *Phalacrocleptes* do not perform the function of feeding and serve for attaching only.

A similar reduction of a part of the tentacles that function as adhesive organelles is also present in *Capriniana piscium* (Bütschli, 1886) inhabiting the gills of freshwater fishes (Batisse, 1994).

There are special funnel-like tentacles in *Choanophrya infundibulifera* (Fig. 25, L) inhabiting cyclopid crustaceans and feeding on fluid remains of host's meals. Haptocysts, a knob and a layer of microtubules are absent in the tentacle (Hitchen and Butler, 1973).

Aside from the adhesive tentacles of *Capriniana piscium*, there are other examples of functional and morphological differentiation of suctorian tentacles. To illustrate, the basal branched tentacles of *Niscometes*

*peregrinus* (Small et Lynn, 1985) (Fig. 29, F) are probably one more case of adhesive organelle. However, morphological differentiation of tentacles is most commonly associated with the separation of functions of prey capture and feeding.

For example (Kahl, 1934), there are both ordinary clavate and lengthened contractile tentacles in podophryid suctorian *Luxophrya limbata* (Maupas, 1881). The latter are furnished with knobs that bear the most of the haptocysts. These tentacles are specialised in capture and transport of the prey to the ordinary "sucking" tentacles (Kahl, 1934; Batisse, 1994).

An analogous specialization is much more exhibited in *Acinetopsis rara* Robin, 1879 (Fig. 24, I). This suctorian feeds on *Ephelota* spp. that is often far greater than the predator. There are one or two hunting tentacles in *Acinetopsis* Robin, 1879, whereas the remainder of the tentacles are much smaller and bear knobs devoid of haptocysts. The prehensile tentacles are ordinary in structure but, on the contrary, gigantic, very lively and enriched with haptocysts (Grell and Meister, 1982).

In contrast, the hunting tentacles of ephelotid suctorians differ from sucking tentacles both in ultrastructure and genesis. The ephelotid clavate sucking tentacles are morphologically ordinary. The prehensile tentacles are devoid of knobs and their axonema pattern is due to the structure formed by sets of long and short semiring chains of microtubules close to each. The axonema begins from special invaginations in macronucleus protrusions and reaches the terminal part of the tentacle (Fig. 10). The haptocysts are numerous along its length (Mikrjukov, 1997).

All modes of tentacles listed (except prehensile tentacle of ephelotids that not homologous to other suctorian tentacles) may be classified into five major groups:

1. The tentacles of *Parapodophrya*, *Lecanophrya*, *Urnulla*, etc., the hunting tentacles of *Acinetopsis* and adhesive tentacles of *Capriniana* Strand, 1928 that are modifications of the clavate tentacle.

2. The funnel-like tentacles of *Choanophrya infundibulifera*, that represent a special case of specialisation to the character of food.

3. The tentacles of *Manuelophrya*, *Pseudogemma*, *Enchelyomorpha*, *Stylocometes*, etc., that may fit into the group of rod-like tentacles. Into this group also the adhesive tentacle of *Phalacrocleptes* may probably fit. By convention (until electron microscopical investigation) we relegate to rod-like tentacles also the larval organelle of endosphaeriid suctorians – the perforatorium.

4. The endosprits of cyathodiniid suctorians, which are an extreme case of specialization of rod-like tentacles, but must be classified into a separate group.



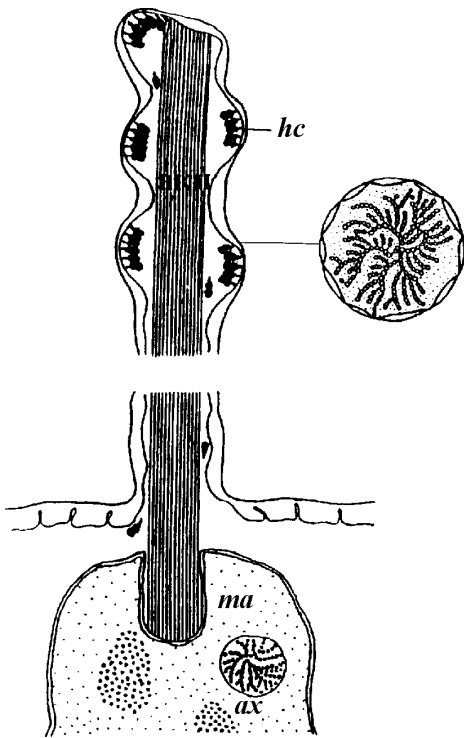


Fig. 10. The fine structure (schematic drawing) of the prehensile tentacle of *Ephelota gemmipara* (Hertwig, 1875) (according to Mikrjukov, 1997). Abbreviations: ax – axonema; hc – haptocyst aggregations; ma – macronucleus.

5. The branched tentacles that are characteristic only for dendrocometids and one ophryodendrid genus (*Shyzactinia*).

Besides tentacles, tentacle-bearing body protuberances called actinophores are often involved into the suctorian feeding apparatus. Conical actinophores situated on the apical body surface are the most widespread. There are also hemispherical, circular and vane-like actinophores. Long contractile actinophores (trunks) of ophriodendrid suctorians are probably the most notable.

Data on the evolution of suctorian tentacles are few in the literature. According to A.V. Jankowski's (1967b) hypothesis, the feeding apparatus development in Suctorea followed two main directions: towards branching of tentacles and towards their polymerization. The polymerization in turn was rendered possible in three ways: 1) when the body retains its simple outlook (as in acinetids); 2) when the body becomes star-shaped and the body edges become wavy (as in trichophryids); 3) when the body becomes branching (*Dendrosoma* Ehrenberg, 1838, *Dendrosomides* Collin, 1906, etc.). In the parasitic suctorian species the feeding apparatus shows a tendency towards oligomerization (Jankowski, 1967b).

We believe that the presence of clavate tentacles in podophryid suctorians and their presence in all large taxa (with different modes of budding) of Suctorea testified to the fact that this mode of tentacles is initial. For example, C.F. Bardele (1972) who investigated the ultrastructure of the tentacles viewed the terminal parts of both rod-like and branched tentacles as reduced knobs of clavate tentacles. In the ramified tentacle of *Dendrocometes paradoxus* the axonemas of individual branching do not merge beneath the point of ramification (Bardele, 1972). This probably means that ramified tentacles are the result of the confluence of several adjacent rod-like tentacles.

Transition from primary clavate tentacles to rod-like ones and from latter to branched tentacles may be considered as a basic tendency in evolution of the suctorian feeding organelle (Fig. 11). In this way the tentaculous apparatus has formed parallelly in different groups by means of specialization to different food objects or to inhabiting various substrates.

Another tendency is division of functions on the basis of polymerization of the organelle. A typical case is the divergence of the tentacles into sucking and hunting ones, the most prominent example being the prehensile tentacle of *Acinetopsis*.

In the several groups of suctorians the tentacles have divided into sucking and adhesive ones. However, in contrast with case just mentioned their functional division was associated with the reduction of both extrusomes and the inner layer of axonema.

Finally, in parasitic suctorians the tendency to oligomerization of the tentacles is characteristic. In this way a single tentacle with a reduced axonema evolved independently in manuelophryids (reproducing by exogemmy) and pseudemmids (with endogemmic budding). The endosphaeriids (with endogemmy) that are mainly intracellular parasites of ciliates and also include the parasite of rotifer tissue *Tripanococcus rotiferorum* Stein, 1867 (with inversogemmy) lost tentacles and transited to osmotrophy in parallel.

A further consequence of polymerization is the transition from irregular distribution of tentacles on the body surface to their association in fascicles or rows. The formation of ctinophores was also associated with this.

As evidenced by the foregoing, the main tendencies in development of tentacles, budding and adhesive organelles are manifest in different and probably not related groups of suctorians. In our opinion, the transfer to commensalism and parasitism on invertebrate hosts makes played the main role in speciation in Suctorea.

Ancestral suctorians were probably similar to recent podophryids. They have in parallel transited to inhabiting different mobile hosts and various modes of

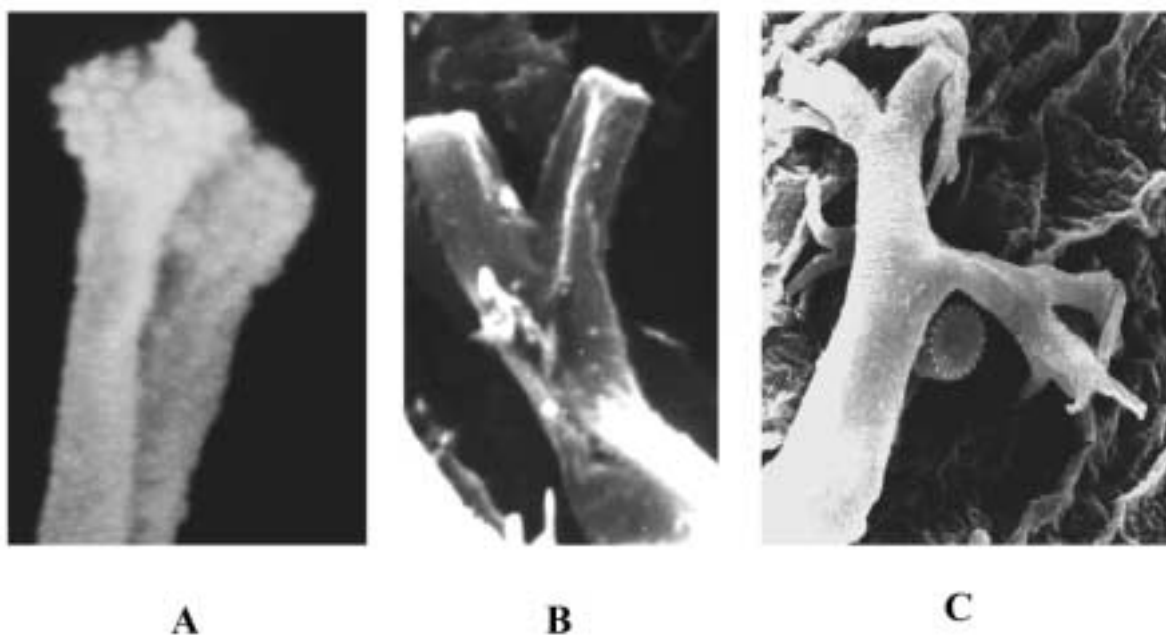


Fig. 11. Evolutionary lineage of suctorian tentacles. A – capitate tentacles of *Periacineta buckei* (Kent, 1882) (SEM, x15000); B – rod-like tentacles of *Stylocometes digitatus* (Claparede et Lachmann, 1859) (SEM, x4400); C – ramified tentacle of *Dendrocometes paradoxus* Stein, 1851 (SEM, x2000).

budding have been developed. The ensuing development of adhesive organelles, feeding apparatus and associated

structures proceeded in suctorian taxa with different types of asexual reproduction independently.

### CHAPTER 3. THE TAXONOMY OF SOME PROBLEMATIC SUCTORIAN GENERA AND SPECIES

Since the publications of identification keys of marine (Kahl, 1934) and freshwater (Matthes et al., 1988) suctorians the revision of suctorian systematics and nomenclature on the generic and species levels has not been conducted. Several important articles on taxonomy of various genera and families have been published at the same time (Curds, 1985a, 1985b, 1985c, 1986, 1987; Rieder, 1985, 1988, etc.). In the last three decades a great number of new genera and species of suctorians have been described. An especially rich variety of taxa has been proposed by A.V. Jankowski (1973a, 1978, 1981, 1982, 1987). Some of the taxa proposed by A.V. Jankowski were taken for granted by other investigators (Batisse, 1994; Dovgal, 1996), but several genera were synonymized or (Matthes et al., 1988) were not mentioned at all.

Prior to the overall revision of suctorian systematics, the taxonomical status and nomenclature of several controversial genera and species should be discussed. The synonymization of suctorian taxonomic names justified by authors (Curds, 1985a, 1985b, 1985c, 1986, 1987; Jankowski, 1987; Matthes et al., 1988; Aescht, 2001) is not discussed here.

Our study of suctorian diagnostic characters disclosed that some of them are impractical, at least for differentiation of genera. For example, the extent of manifestation of several characters (the degree of lorica development, asymmetry of lorica, thickness of its walls, the degree of stalk-like stylothea protuberance or stalk development and apical stalk widening, etc.) may be associated with the extent to which the tectin secretion proceeds during morphogenesis. These characters are often considerably variable. Such characters as presence or absence of lorica folds and ribs, the shape of trophont cell body and tentacle thickness have possibly evolved independently in different taxa. In this case they do not point at the affinity between these taxa. For this reason we do not accept several genera that were introduced using characters listed.

Arrangement and number of the tentacles or tentacle fascicles may at times be reliable characters for classification of genera (as in allantosomid or acinetid suctorians). At other times they are limited to interspecific variability (as in discophryid and tokophryid suctorians).

In all instances it is good practice to accept genera if their elevation was founded on a combination of characters and not on a single character.

**GENUS *SPHAEROPHYA* CLAPAREDE  
ET LACHMANN, 1859**

This genus includes planktonic and parasitic suctorians that are devoid of stalk (Fig. 19, C). Currently this generic name is often used as the younger synonym of *Podophrya* Ehrenberg, 1834 because of the similarity in cyst morphology and the presence of stalked stages in the life cycle of parasitic sphaerophrians (Jankowski, 1963). However, in a famous work by Matthes et al. (1988) the genus was accepted as different from *Podophrya* in absence of stalk and structure of cysts. We also believe that the representatives of *Sphaerophrya* are different enough from *Podophrya* to relegate them into a separate genus. The similarity of cyst structure attests the affinity between the genera but is not a good reason for their synonymization.

**THE SYSTEMATIC POSITION OF *ALLANTOSOMA*  
*MULTISUCTORES* VAN HOVEN ET AL., 1998**

A new suctorian species (*Allantosoma multisuctores*, Fig. 19, D) was reported from the intestine of black and white wild African rhinoceroses (Van Hoven et al., 1998). From 20 to 24 clavate tentacles unevenly arranged at the cell surface are characteristic for the species. The relative position of tentacles is a generic character in Allantosomatidae Jankowski, 1978. Allantosomid genera with different arrangement of tentacles are accepted by specialists (see Batisse, 1994).

*A. multisuctores* differs from other allantosomids by the fact that its tentacles are scattered over entire body surface instead of being confined to cell poles. For this reason the species might be even assigned to podophryid suctorians. However, a specific pattern of axonema mictorubules is characteristic for allantosomid suctorians (Sundermann and Paulin, 1981) and it can be assumed that the axonema of *A. multisuctores* tentacles has a similar pattern. Therefore we believe that *A. multisuctores* is an allantosomid suctorian and must be relegated to a new genus *Vanhovenia* gen. n. Generic name is given in honour of Dr. Wouter Van Hoven, University of Pretoria, South Africa.

**GENUS *VANHOVENIA* DOVGAL, GEN. N.**

The suctorian ciliate with an ellipsoid-like body. Several clavate tentacles are distributed all over the cell body. Macronucleus is spherical and centrally placed.

There is a single contractile vacuole. The new genus differs from related allantosomid genera (*Allantosoma* Gassowki, 1918, *Arcosoma* Jankowski, 1967 and *Allantoxena* Jankowski, 1978) by the arrangement of tentacles and localization in intestine of rhinoceroses instead of equines. Type species: *Allantosoma multisuctores* Van Hoven et al., 1998 (Fig. 19, D).

**GENUS *DISCACINETA* JANKOWSKI, 1981**

The genus *Discacineta* has been proposed by A.V. Jankowski (1981) for the representatives of the genus *Metacineta* Bütschli, 1889 with stylothea devoid of a stalk-like protuberance. The type species of the genus is *Solenophrya micraster* Penard, 1914. Literary data (Rieder, 1985) and our observations demonstrate that the individuals of the type species with short protuberance of lorica can occasionally be found. The rest of the characters are identical with *Metacineta*. Therefore it is not necessary to elevate a separate genus for these forms. The name *Discacineta* Jankowski, 1981 is synonymized with *Metacineta* Bütschli, 1889.

**GENUS *DELTACINETA* JANKOWSKI, 1981**

The genus *Deltacineta* has been proposed by A.V. Jankowski (1981, p. 96) for the paracinetid suctorians with laterally flattened stylothea with a short stalk-like protuberance. The type species of the genus is *Deltacineta seticola* Jankowski, 1981. On page 94 of the article mentioned a new genus *Limnoricus* Jankowski, 1981 has been described with the same characters but with stylothea with a long stalk-like protuberance. It is our opinion that the length of adhesive structure is not a character but only its state. We believe that *Deltacineta* is a younger synonym of *Limnoricus* and the species *Deltacineta seticola* Jankowski, 1981 must be transferred in the genus *Limnoricus* Jankowski, 1981.

**GENUS *LORICOPHYA* MATTHES, 1956**

The genus *Loricophrya* has been elevated by D. Matthes (1956) for several species of *Thecacineteta* Collin, 1909 with unrecognized mode of budding. The type species of the genus is *Thecacineteta parva* Schulz, 1932 (Fig. 20, E).

In our opinion quite a lot of genera might be characterized like this, since budding is not investigated in many suctorian species. Nevertheless, the genus was accepted by many specialists (see Curds, 1987).

More recently A.V. Jankowski (1978) has proposed a new genus *Heliothea* Jankowski, 1978 for the «loricate forms with apical tentacles» and with the type species *Thecacineteta caepula* Penard, 1920. The

reproduction of the type species is not investigated and it has been transferred in *Loricophrya* (Curds, 1987).

D. Matthes' diagnosis of *Loricophrya* was supplemented by a morphological character (Curds, 1987). The latter author indicated that the stalk-like protuberance of lorica in loricophryans is shorter than the lorica itself. But *Acineta bifaria* Stokes, 1887 was transferred in the genus and the type of budding is known for the species. This is in conflict with Matthes' characteristic of genus, i.e. unknown mode of budding.

*A. bifaria* reproduces by exogemmic budding with apical protomit position. The swarmer morphology is similar with podophryid or paracinetid suctorians, i.e., its body shape is elongate-cycloid with several longitudinal kineties and tentacles.

It should be mentioned that the same mode of reproduction and bud morphology is characteristic of the suctorian *Solenophrya sacculus* Penard, 1914. It is very similar to *A. bifaria*, differing only by the absence of the stalk and the characteristic inlay of the lorica. It is possible that the absence of the stalk-like protuberance of the lorica is the case of intraspecific variability as in *Metacineta micraster* (Penard, 1914) and incrustation of the lorica may be result of its overgrowing by diatoms. It is unquestionable that these species must be assigned to *Loricophrya*.

Most likely C. Curds (1987) believed that all representatives of *Loricophrya* have the same mode of reproduction as *Acineta bifaria* and for this reason discussed the genus as related to *Paracineta* Collin, 1912. This idea can be supported by the fact that, as W. Foissner (1995) indicated, yet another species of the genus – *L. lauterborni* (Sondheim, 1929) has the same mode of budding. From the above it is clear that *S. sacculus* Penard, 1914 must be transferred in *Loricophrya*<sup>3</sup>. The diagnosis of the genus might be improved as follows:

#### GENUS *LORICOPHYA* MATTHES, 1956

Freshwater, marine and soil suctorians with the stylotheca. The stalk-like protuberance of stylotheca is shorter than the lorica itself and may absent. The cell body spherical or ellipsoid. Macronucleus spherical or elongated. Several clavate tentacles are arranged at the apical surface of the body. Reproduction by exogemmy with formation of a single apical protomit. Swarmer oval with longitudinal ciliary rows and tentacles. Type species: *Thecacineta parva* Schulz, 1932 (Fig. 20, E).

#### GENERA *PSEUDOGEMMIDES* KORMOS, 1935, *MISTARCON* JANKOWSKI, 1986 AND *MANUELOPHYRYA* MATTHES, 1988

The species of loricate ectoparasite described by J. Kormos (1935b) from suctorian *Periacineta* sp. Exogemmy (semi-circumvaginate budding) is characteristic for the new species (distinguished from morphologically related representatives of the genus *Pseudogemma* with endogemmy) and on this basis a new genus *Pseudogemmides* was proposed by author. The type species of the genus is *Pseudogemmides globosa* Kormos, 1935 (Fig. 20, H). More recently (Kormos and Kormos, 1958) the name *Pseudogemmides* was synonymized with *Urnula* Claparede et Lachmann, 1861. However, the representatives of the latter are metacinetid suctorians with a single extremely long and agile tentacle unlike the short rod-like one in *Pseudogemmides*. Thus it is unlikely that this taxonomical action is justified. Nevertheless, some authors (Matthes et al., 1988; Jankowski, 1997) accepted it. A. Batisse (1994), in turn accepted both *Pseudogemmides* and *Urnula*.

One further ectoparasitic species was described by K. Nozawa (1939) under the name *Pottisia parasitica* Nozawa, 1939 (Fig. 20, G). The individuals of the species are parasites of peritrichous ciliates, attaching to the host's bell by rod-like tentacles and to the host's stalk by a short protuberance of the lorica. Consequently these ciliates are located only near the junction between stalk and zooid. J. Corliss (1960) proposed for the name *Pottisia* Chatton et Lwoff, 1927 the substituted name *Pottsiocles* in connection with homonymy. However, subsequently it was found that K. Nozawa's species is unrelated to the genus *Pottsiocles* since it has rod-like tentacle and not capitate ones. Thus *P. parasitica* was transferred into *Pseudogemmides* Kormos (Dovgal, 1988, 1991, 1996).

A.V. Jankowski (1986) proposed to classify *Pottisia parasitica* into a new taxon but without refinement of its taxonomical rank. According to the author's primary description (Jankowski, 1986, p. 85): "*Mistarcon* is the new genus or subgenus of *Pseudogemmides* Kormos, 1935". A.V. Jankowski also proposed to use one or the other combination of names "as specialists deem necessary". Finally, in a review article dealing with the problem of *Mistarcon* and related genera (Jankowski, 1997) the detailed diagnosis of the genus is given. The presence of protuberance of the lorica ("bearing plate") by which the suctorian attaches to the host's stalk is indicated as a characteristic of the genus.

A new species with rod-like tentacles was described by W. Guhl (1985) under the name *Pottsiocles hanna* (Fig. 20, I). The species was transferred into *Pseudogemma* on the basis of the tentacle type (Dovgal, 1991).

<sup>3</sup> All new combinations of the names and synonyms are indicated in Chapter 5.

W. Guhl's species was classified (Matthes et al., 1988) along with *Pottisia parasitica* with exogemmic budding in the new genus *Manuelophrya*. The type species of *Manuelophrya* was not indicated by the author. A.V. Jankowski (1992, 1997), in turn indicated *Pottsiocles hanna*e Guhl, 1985 as the type species of *Manuelophrya*.

It should be noted that at first glance *Manuelophrya* is not morphologically different from *Pseudogemmides*. However, the presence of lorica was not mentioned either in the diagnosis of type species of the genus *Pseudogemmides* (*P. hanna*e) or in the diagnosis of the genus *Manuelophrya* (see Matthes et al., 1988). Consequently, there is a sufficient distinction between *Manuelophrya* and *Pseudogemmides* and both the genus of J. Kormos' and that of D. Matthes' genera should be reclaimed.

We accept three related genera for parasitic exogemmins with rod-like tentacles as the result: *Pseudogemmides* Kormos, 1935 (type species is *P. globosa* Kormos, 1935, Fig. 20, H) possessing the lorica and attaching to host's cell by the tentacle; *Mistarcon* Jankowski, 1986 (type species is *Pottisia parasitica* Nozawa, 1939, Fig. 20, G) possessing the lorica and attaching to host's body by the tentacle and to host's stalk by lorica protuberance, and *Manuelophrya* Matthes, 1988 (type species is *Pottsiocles hanna*e Guhl, 1985, Fig. 20, I) without lorica, attaching to the host's zooid by the tentacle.

#### GENUS *MIRACINETA* JANKOWSKI, 1981

The new genus *Miracineta* has been elevated by A.V. Jankowski (1981) for paracinetid suctorians with thickened bottom of the stylothea. The type species of the genus is *Acineta saifulae* Mereschkowsky, 1877. In our opinion the character "thickness of lorica bottom" is not generic. The name *Miracineta* Jankowski, 1981 is synonymized with the *Paracineta* Collin, 1912.

#### GENUS *FLECTACINETA* JANKOWSKI, 1978

The genus *Flectacineta* was proposed by A.V. Jankowski (1978) for paracinetid suctorians "with stylothea and apical tentacles". The type species of the genus is *Acineta livadiana* Mereschkowsky, 1881 (Fig. 7, Bb). The genus was accepted by C. Curds (1987), who amplified the diagnosis by the characteristic of lorica rim that is "inverted at apex, mounted upon a hollow stalk". We investigated the type species of the genus. According to our observations the majority of individuals actually have the characteristic inversion of the stylothea rim but there is a considerable variability of this character. There is good probability

that the same morphology of the stylothea might have emerged in the several related species in parallel and is accordingly unsuitable for erection of the new genus. The name *Flectacineta* Jankowski, 1978 is synonymized with the *Paracineta* Collin, 1912.

#### GENUS *FALTACINETA* JANKOWSKI, 1981

For A.V. Jankowski's (1981) opinion those representatives of the genus *Paracineta* that have irregular folded stylothea must be classified in the separate genus *Faltacineta*. *Paracineta pleuromammae* Steuer, 1928 has been designated as the type species. We believe that the outline of lorica is not sufficient for the erection of the genus. The name *Faltacineta* Jankowski, 1981 must be synonymized with *Paracineta* Collin, 1912.

#### GENUS *SARGASSEPHELOTA* JANKOWSKI, 1981

The genus *SargassepHELota* has been erected by A.V. Jankowski (1981) for ephelotid species with prehensile tentacles arranged in a basal ring. The type species of the genus is *Ephelota butschliana* Ishikawa, 1897. In our opinion the arrangement of tentacles is not a good reason for separation of the genus in ephelotid suctorians. The name *SargassepHELota* Jankowski, 1981 is synonymized with *Ephelota* Wright, 1859.

#### GENUS *DISCEPHELOTA* JANKOWSKI, 1981

The new genus *DiscepHELota* was erected by A.V. Jankowski (1981) for ephelotid suctorians with massive apical widening of stalk. The type species of the genus is *Ephelota gigantea* Noble, 1929. Apical enlargement of the stalk is in fact widely distributed in ephelotids and could not be used for elevating the genus. The name *DiscepHELota* Jankowski, 1981 is the younger synonym of *Ephelota* Wright, 1859.

#### THE SYSTEMATIC POSITION OF *PODOCYATHUS EXCAVATUS* DONS, 1938

This species described by C. Dons (1938) has a deep cavity on the apical body surface. This feature makes *Podocyathus excavatus* similar to the type species of *MetepHELota* Willis, 1945, the latter possessing a large apical cavity of the body in which the several sucking tentacles are placed. A.G. Willis (1945) noted the similarity between *P. excavatus* and *M. coronata* Willis, 1945 (Fig. 21, C). However, in the opinion of this author the transferring of *P. excavatus* in the genus *MetepHELota* was premature. More recently, A.V. Jankowski (1981) erected *P. excavatus* in separate genus *Discocyathus*

based on the presence of the apical stalk widening that is equal to the cell width. In our view the degree of development of the character that is common in many ephelotid species cannot serve as a basis for elevation of a new genus. On the other hand, we believe that there is good reason to transfer *P. excavatus* in the genus *Metephelota*. The name *Discocyathus* Jankowski, 1981 is respectively the younger synonym of *Metephelota* Willis, 1945.

#### GENUS *STYLOGEMMA* JANKOWSKI, 1981

The genus *Stylogemma* has been erected by A.V. Jankowski (1981) for rhabdophriid suctorians that are related to genus *Trophogemma* Jankowski, 1970 but have a cylindrical stalk instead of a pedicle. The type species of the genus is *Rhabdophrya wailesi* Kahl, 1934. The differentiation between stalk and pedicle amounts to the degree of character development and cannot be the reason for erection of the genus.

It should be recognized that there are two actinophores in *R. wailesi*. A. Kahl (1934) has described these structures as «buds». The same actinophores are actually characteristic of *Trophogemma* but *R. wailesi* has capitata tentacles in contrast with rod-like ones in *Trophogemma*. At the same time, the representatives of the genus *Dendrosomides* Collin, 1906 have a combination of characters similar to *R. wailesi* (well-developed actinophores bearing capitata tentacles). In our opinion a supplementary investigation of *R. wailesi* morphology is necessary. As yet the species is transferred into the genus *Dendrosomides*. Consequently, the name *Stylogemma* Jankowski, 1981 is synonymized with *Dendrosomides* Collin, 1906.

#### THE SYSTEMATIC POSITION OF *OPHRYODENDRON MYSIDACII* FERNANDEZ-LEBORANS ET AL., 1996

A new species of vermigemmin suctorian *Ophryodendron mysidacii* (Fig. 22, D) has been described by G. Fernandez-Leborans et al. (1996) as commensal of mysids from the estuary of river Bidasoa (Spain). The species differs significantly from the other representatives of the genus *Ophryodendron* Claparede et Lachmann, 1859 by the presence of clavate tentacles and the lack of contractile actinophore (“trunk”) typical for ophryodendrid suctorians. There are good reasons for transferring *O. mysidacii* into the family Dendrosomididae Jankowski, 1981. However, the species differs from the representatives of the type genus of this family (*Dendrosomides* Collin, 1906) by the presence of elongated unramified macronucleus and the lack of the stalk (present in attached swarmer). By the latter character *O. mysidacii* differs from the all

dendrosomidid species. We believe that *O. mysidacii* should be relegated into a separate genus *Leboransia* gen. n. Generic name is given in honour of Dr. Gregorio Fernandez-Leborans.

#### GENUS *LEBORANSIA* DOVGAL, GEN. N.

Vermigemmin suctorians with a bag-shaped body elevated or sprawled over the substrate. The organism attaches to the substrate by the basal part of the body. Capitata tentacles are placed on 4-7 actinophores. The macronucleus is ribbon-like. The representatives of the genus reproduce by vermigemmy with formation of a single lateral protomit. The swarmer is devoid of ciliature and equipped with a larval adhesive organelle (sucker) located in the anterior pole. After attachment the swarmer forms a temporary stalk. The cyst is elliptic with a thin cover and attached to the substrate by a short basal protuberance. Type species: *Ophryodendron mysidacii* Fernandez-Leborans et al., 1996 (Fig. 22, D).

#### GENUS *DENTACINETIDES* BATISSE, 1992

The genus *Dentacinetides* with the type species *Dentacinetides collini* Batisse, 1992 has been described by A. Batisse (1992). The genus is very similar to *Dentacineta* Jankowski, 1978 and differs from the latter only by number of cortical ribs of the trophont body (6 in *Dentacineta* and 8 in *Dentacinetides* respectively). In our view this is not a good reason for elevation of a separate genus. We believe that the name *Dentacinetides* Batisse, 1992 is a younger synonym of *Dentacineta* Jankowski, 1978. Consequently the species *Dentacinetides collini* Batisse, 1992 must be transferred into the genus *Dentacineta*.

#### THE SYSTEMATIC POSITION OF GENUS *PLEUROPHRYODENDRON* JANKOWSKI, 1978

The genus *Pleurophryodendron* has been erected by A.V. Jankowski (1978) for ophryodendrid suctorians with semi-internal budding. The type species of the genus is *Ophryodendron reversum* Collin, 1909 (Fig. 22, F) from the harpacticoid copepod *Ameira* sp. According to B. Collin's (1909, 1912) diagnosis and figures the organism has an unflattened body with a long stalk. The tentacles and actinophores are absent but in one of B. Collin's (1912) figures a thick fibrillar structure can be seen, considered by the author as a withdrawn “proboscis” (actinophore). The reproduction (consecutive polygemmic vermigemmy) begins with a rather shallow invagination of cortex at the lateral surface of the body.

In our opinion, as to the body shape and the manner of budding *O. reversum* is rather similar to

representatives of *Dentacineta* Jankowski, 1978 that also inhabit *Ameira* sp. and reproduce by vermigemmy. This species differs from dentacinetid by the formation of the protomit in a cell invagination and by successive budding. It is profitable to transfer the genus *Pleurophryodendron* Jankowski, 1978 into the family Dentacinetidae Batisse, 1992. The diagnosis of the genus given by A.V. Jankowski is not very informative and might be refined as follows:

#### GENUS *PLEUROPHRYODENDRON* JANKOWSKI, 1978

The vermigemmin marine suctorians with unflattened pyramidal body. The macronucleus is spherical or elongated. Lorica is absent. There is a long slightly curved stalk. Tentacle morphology is unknown. Reproduction is by semi-internal successive vermigemmy. The vermiform swarmer is devoid of ciliature. Type species: *Ophryodendron reversum* Collin, 1909 (Fig. 22, F).

#### GENUS *LISSACINETA* JANKOWSKI, 1981

The genus *Lissacineta* has been proposed by A.V. Jankowski (1981) for representatives of *Thecacineteta* that have the lorica without folds. The *Thecacineteta cothurnioides* Collin, 1912 has been indicated as the type species. In our view the character mentioned is no a good cause for elevation of a separate genus and the name *Lissacineta* Jankowski, 1981 is synonymized with *Thecacineteta* Collin, 1909.

#### GENUS *LITACINETA* JANKOWSKI, 1978

The genus *Litacineta* has been erected by A.V. Jankowski (1978) for thecacinetid suctorians that have the lorica with several apical ribs. The type species of the genus is *Thecacineteta gracilis* Wailes 1928. This character cannot be used for elevating of the genus. The name *Litacineta* Jankowski, 1978 is a younger synonym of *Thecacineteta* Collin, 1909.

#### GENUS *PARADENTACINETA* JANKOWSKI, 1978

The genus *Paradentacineta* has been elevated by A.V. Jankowski (1978) for representatives of *Thecacineteta* "with the tentacles as in acinetiens". The type species is *Thecacineteta cypridinae* Collin, 1912. In our view capitate tentacles are common in many thecacinetids and the character cannot serve as a basis for elevation of a new genus. The name *Paradentacineta* Jankowski, 1978 is a younger synonym of *Thecacineteta* Collin, 1909.

#### GENUS *STYLARCON* JANKOWSKI, 1981

The new genus *Stylarcon* has been elevated by A.V. Jankowski (1981) for rhabdophryid suctorians with the tentacles arranged in transverse and diagonal rows. The *Rhabdophrya truncata* Dons, 1918 has been indicated as a type species of the genus. In our opinion the arrangement of tentacles is not a generic character in Rhabdophryidae Jankowski, 1978. The name *Stylarcon* Jankowski, 1981 is a younger synonym of *Rhabdophrya* Chatton et Collin, 1910.

#### GENUS *STYLOSTOMA* MILNE, 1886

The genus *Stylostoma* that includes ophryodendrid suctorians with several actinophores was not accepted by protozoologists but A.V. Jankowski (1967a) restored it and supplemented the diagnosis by indication that the actinophores are not folded (Jankowski, 1981). The *Acineta trinacria* Gruber, 1884 has been indicated as a type genus. The polymerization of the "trunk" is a common characteristic in many ophryodendrids and cannot serve as a basis for erection of a separate genus. The name *Stylostoma* Milne, 1886 must be synonymized with *Ophryodendron* Claparede et Lachmann, 1859.

#### GENUS *THISARCON* JANKOWSKI, 1981

The genus *Thisarcon* have been erected by A.V. Jankowski (1981) for the ophryodendrid suctorians with a broadened body and a flattened apical cell surface possessing from 4 to 6 actinophores. The type species of the genus is *Ophryodendron conicum* Schröder, 1907. It is our belief that body outlines only are not sufficient for elevation of a new genus. The name *Thisarcon* Jankowski, 1981 must be synonymized with *Ophryodendron* Claparede et Lachmann, 1859.

#### GENUS *ELITARCON* JANKOWSKI, 1981

The new genus *Elitarcon* has been described by A.V. Jankowski (1981). The type species of the genus is *Elitarcon harmothois* Jankowski, 1981. As a basic generic characteristic the presence of several folded actinophores was indicated. It has already been noted here that the polymerization of actinophores is not a generic character for ophryodendrid suctorians. The name *Elitarcon* Jankowski, 1981 is a younger synonym of *Ophryodendron* Claparede et Lachmann, 1859. The species *E. harmothois* must be transferred into the genus *Ophryodendron*.

**GENUS NEMERTODENDRON JANKOWSKI, 1978**

In the primary diagnosis of the genus *Nemertodendron* only the presence of several apical actinophores has been indicated as a basic character (Jankowski, 1978). As the type species of the genus *Ophryodendron prenanti* Duboscq, 1925 has been marked. The diagnosis was subsequently supplemented (Jankowski, 1981) with evidence that in representatives of the genus the actinophores are not ribbon-like, thin, tubular and bear several hooked tentacles on the ends.

In our view the characters mentioned are not sufficient for elevation of a separate genus. The name *Nemertodendron* Jankowski, 1978 is synonymized with *Ophryodendron* Claparede et Lachmann, 1859.

**GENUS STYLOPHRYODENDRON JANKOWSKI, 1978**

The genus *Stylophryodendron* has been elevated by A.V. Jankowski (1978) for stalked ophryodendrid suctorians. The type species is *Ophryodendron roscoffensis* Batisse et Dragesco, 1967. Ophryodendrid suctorians that are devoid of stalk are classified in the separate genus *Corethria* Wright, 1861 and as a result only stalked species remain in the genus *Ophryodendron*. Consequently, it is not necessary to erect a new genus with the same diagnosis. The name *Stylophryodendron* Jankowski, 1981 is a younger synonym of *Ophryodendron* Claparede et Lachmann, 1859.

**GENUS SETARCON JANKOWSKI, 1981**

A.V. Jankowski (1981) has proposed to relegate the ophryodendrid suctorians with stalk and sole actinophore in a new genus *Setarcon*. The *Ophryodendron pedicellatum* Hincks, 1873 was indicated as the type species. As mentioned above, the number of actinophores is not a generic character in ophryodendrids. The name *Setarcon* Jankowski, 1981 is synonymized with *Ophryodendron* Claparede et Lachmann, 1859.

**GENUS ISOPODARCON JANKOWSKI, 1981**

A.V. Jankowski (1981) has classified the ophryodendrid species with "polymerization of actinophores" into a separate genus *Isopodarcon*. The type species is *Ophryodendron multicapitatum* Kent, 1881. We do not accept this character as generic in Ophryodendridae and synonymize the name *Isopodarcon* Jankowski, 1981 with *Ophryodendron* Claparede et Lachmann, 1859.

**GENUS SYLLARCON JANKOWSKI, 1981**

A new genus *Syllarcon* with type species *Syllarcon draconematis* Jankowski, 1981 has been described by

A.V. Jankowski (1981). The location of several tentacles only on the top of the actinophore was indicated as a basic character of the genus. Several species from the genus *Ophryodendron* have been transferred into the new genus by A.V. Jankowski. The arrangement of tentacles on the actinophore is of no value for description of genera in ophryodendrid suctorians. Consequently, the name *Syllarcon* Jankowski, 1981 is the younger synonym of *Ophryodendron* Claparede et Lachmann, 1859. The species *S. draconematis* is transferred into the genus *Ophryodendron* respectively.

**GENUS VINARCON JANKOWSKI, 1981**

The new ophryodendrid genus *Vinarcon* with the type species *Vinarcon asteris* Jankowski, 1981 (from echinoderms) has been described by A.V. Jankowski (1981). The presence of a specific structure (ampoule) at the basal part of body and the lack of polymerization of the actinophore are the characteristics of the genus. In our view the number of actinophores is not a genetic character in Ophryodendridae and a supplementary investigation of the attachment structure of the type species is necessary. The adhesion to the substrate is effected in *V. asteris* by the basal protuberance of the body. The lack of the stalk is characteristic for the genus *Corethria* Wright, 1861. The name *Vinarcon* Jankowski, 1981 is synonymized with *Corethria* and *V. asteris* transferred into the latter genus.

**GENUS TRINACINETA JANKOWSKI, 1981**

A.V. Jankowski (1981) proposed to classify the species of tokophryid suctorians with three fascicles of the tentacles into a new genus *Trinacineta*. The type species of the genus is *Podophrya diaptomi* Kellicott, 1885. The above mentioned character is rather rare in suctorians of the genus *Acineta* as compared to *Tokophrya*. Consequently, the presence of this character points to the affinity between species and is truly generic for the acinetid suctorians. However, in unloricate tokophryid suctorians, which most commonly have an unflattened body, the species with more than two bundles of the tentacles are much more widespread. Therefore there is little point in erection of a new genus on the basis of polymerization of the tentacle fascicles in tokophryids. The name *Trinacineta* Jankowski, 1981 is a younger synonym of *Tokophrya* Bütschli, 1889.

**THE SYSTEMATIC POSITION OF TESTUDINICOLA GLOBOVATA BOVEE, 1981**

A new species *Testudinicola globovata* has been described by E. Bovee (1981) from American turtles.



*T. globovata* has a spherical body with two apical fascicles of clavate tentacles and a very short stalk. The species has been erroneously assigned by the author to the genus *Testudinicola* Jankowski, 1978, for which the lack of the stalk is characteristic. Recently (Matthes et al., 1988), the type species of the genus *Testudinicola* (*Anarma brevis* Goodrich et Jahn, 1943) has been transferred into the genus *Trichophrya*. However, the above-listed characters of Bovee's species (especially, presence of the stalk) show that the species must be assigned to the genus *Tokophrya* Bütschli, 1889 instead of *Trichophrya*.

#### GENUS *ARMIACINETA* JANKOWSKI, 1982

A new genus *Armiacineta* from gammarid amphipods of Lake Baikal has been described by A.V. Jankowski (1982). The *Armiacineta seticola* Jankowski, 1982 has been indicated as the type species of the genus. The presence of well-developed actinophores and thin, twisted capitate tentacles (named «flexotenes» by the author) were marked as basic characteristics of the genus. However, actinophores are common in tokophryids and «flexotenes» are most probably not a special type of tentacles but only a variation of usual capitate tentacles. The species *A. seticola* must be transferred into the genus *Tokophrya* and the name *Armiacineta* Jankowski, 1982 synonymized with *Tokophrya* Bütschli, 1889.

#### GENUS *SIBIRACINETA* JANKOWSKI, 1982

The presence of allometric stalk widening that comprises the bowl-like bearing structure is a characteristic feature of a new genus *Sibiracineta*. The type species of the genus is *Sibiracineta endemica* Jankowski, 1982 inhabiting Baikal gammarid crustaceans. We emphasize that various structures enhancing the junction between stalk and body are common in Tokophryidae Jankowski, 1978 and cannot serve as a basis for erection of the genus. The name *Sibiracineta* Jankowski, 1982 is the younger synonym of *Tokophrya* Bütschli, 1889. Consequently, *S. endemica* must be transferred into *Tokophrya*.

#### GENUS *TOKOPHRYONA* JANKOWSKI, 1982

The new genus *Tokophryona* with the type species *Tokophryona pelagica* Jankowski, 1982 has been described by A.V. Jankowski (1982) from Baikal alga *Anabaena* sp. The presence of several thin tentacles (flexotenes) was indicated as a characteristic feature of the genus. The oligomerization of tentacles is common among tokophryids and as noted above the «flexotene»

is a variant of usual capitate tentacles. In our view, it is not necessary to elevate a separate genus for such forms. The name *Tokophryona* Jankowski, 1982 is synonymized with *Tokophrya* Bütschli, 1889 and *Tokophryona pelagica* is transferred into *Tokophrya*.

#### GENUS *BASITOKOPHRYA* JANKOWSKI, 1982

A.V. Jankowski (1982) has proposed to elevate the species with an unusual structure at the junction of the stalk and the body in form of a frilled collar-like disc in separate genus *Basitokophrya*. The type species of the genus is *Tokophrya ornata* Gajewskaja, 1933 from gammarid crustaceans of Lake Baikal. As was mentioned above the structures enhancing the stalk-body connection are not generic characters in tokophryans. The name *Basitokophrya* Jankowski, 1982 is a younger synonym of *Tokophrya* Bütschli, 1889.

#### GENUS *NORACINETA* JANKOWSKI, 1978

The genus *Noracineta* has been erected by A.V. Jankowski (1978) for acinetin suctorians “with hollow stalk and thecostyle”. *Acineta infundibuliformis* Wang et Nie, 1933 was indicated as a type species. Earlier in the same article the genus *Anthacineta* Jankowski, 1978 was described with a similar diagnosis but with a “semilorica”. We believe that the degree of the lorica development cannot be a basis for erection of the genus. The name *Noracineta* Jankowski, 1978 is a younger synonym of *Anthacineta* Jankowski, 1978.

#### GENUS *SEMIACINETA* JANKOWSKI, 1978

The new genus *Semiacineta* has been erected by A.V. Jankowski (1978) for acinetid suctorians “with semilorica”. The type species of the genus is *Acineta swarczewskyi* Collin, 1911. The diagnosis given is the same as the one for *Anthacineta*. The name *Semiacineta* Jankowski, 1978 is synonymized with *Anthacineta* Jankowski, 1978.

#### GENUS *CONCHACINETA* JANKOWSKI, 1978

The genus *Conchacineta* was elevated by A.V. Jankowski (1978) for acinetid suctorians with tentacles that are arranged in rows. *Acineta constricta* Collin, 1909 has been indicated as the type species of the genus. The genus *Conchacineta* was accepted by C. Curds (1985a). However, in his article C. Curds does not cite the paper of A. Batisse (1972) in which a new genus *Trematosoma* Batisse, 1972 with a similar diagnosis was erected. In another article (Curds, 1985b) mention has already been made of the fact that

the diagnoses of A. Batisse (1972) and A.V. Jankowski (1978) are nearly identical.

Typical characters of the genus *Trematosoma* are arrangement of the tentacles in rows, position of the tentacle bases in a deep fold and presence of very large alveoles along apical body edge. In our opinion, the key generic character (rows of the tentacles) is the same in *Trematosoma* and in *Conchacineta*. This has led us to believe that *Trematosoma* Batisse, 1972 is a valid name but *Conchacineta*, 1978 is its younger synonym. Consequently, all species assigned by A.V. Jankowski and C. Curds to the genus *Conchacineta* must be transferred into *Trematosoma*.

#### GENUS *SPARSACINETA* JANKOWSKI, 1978

The genus *Sparsacineta* was elevated by A.V. Jankowski (1978) for acinetid suctorians “with semilorica”. As the type species *Acineta complatana* Gruber, 1884 was indicated. In the recent revision of acinetians (Curds, 1985a) the latter species was erroneously mentioned as a representative of the genus *Soracineta* Jankowski, 1978. Respectively, the generic name *Soracineta* was erroneously synonymized with *Conchacineta* Jankowski, 1978 instead of *Sparsacineta* (Dovgal, 1999). We emphasize that the tentacles of *A. complatana* are arranged in rows as characteristic for representatives of the genus *Trematosoma*. Consequently, we believe that the name *Sparsacineta* Jankowski, 1978 is a younger synonym of *Trematosoma* Batisse, 1972.

#### GENUS *RIMACINETA* JANKOWSKI, 1981

For the acinetids with tentacles arranged in rows and a finned lorica A.V. Jankowski (1981) has proposed the genus *Rimacineta* with the type species *Rimacineta falcata* Jankowski, 1981. The structuring of the lorica is not a generic character. We believe that the name *Rimacineta* Jankowski, 1981 is a younger synonym of *Trematosoma* Batisse, 1972. The species *R. falcata* is transferred into *Trematosoma*.

#### GENUS *PLICOPHRYA* JANKOWSKI, 1975

The genus *Plicophrya* was erected by A.V. Jankowski (1975) for the acinetid suctorians with two fascicles of the tentacles and a folded lorica. The type species of the genus is *Acineta sulcata* Dons, 1927. As mentioned above, we do not accept the structuring of the lorica as generic character. The name *Plicophrya* Jankowski, 1975 is synonymized with *Acineta* Ehrenberg, 1834.

#### GENUS *CROSSACINETA* JANKOWSKI, 1978

The genus *Crossacineta* was erected by A.V. Jankowski (1978) for the acinetid suctorians that have an annulate lorica. The type species is *Acineta ornata* Sand, 1899. The genus was accepted by C. Curds (1985a). However, the presence of any folds, rings, fins, etc. of the lorica is not a generic character in our opinion. The name *Crossacineta* Jankowski, 1978 is a younger synonym of *Acineta* Ehrenberg, 1834.

#### GENUS *PSEUDOCORYNOPHRYA* SMALL ET LYNN, 1985

The new genus *Pseudocorynophrya* was described by E. Small and D. Lynn (1985) without indication of the localities. The host of the suctorian is a crustacean *Rhinocalanus* sp. In the authors' opinion, typical characteristics of the genus are the trumpet-shaped body and arrangement of the groups of tentacles on the distal cell surface. The type species was not indicated, but *Pseudocorynophrya multitentaculata* Small et Lynn, 1985 must be pointed as the type species on the basis of monotypy. In the species diagnosis a lorica on a stalk was also mentioned.

Judging from the figure of the species given by the authors (Small and Lynn, 1985, Fig. 26, p. 503) this suctorian lacks the lorica. The authors appear to have mistaken for the lorica the apical widening of the stalk. The macronucleus morphology and reproduction were not observed. In our opinion, on the strength of the such characters as laterally unflattened body, positioning of the tentacles on its apical surface and the presence of the apical stalk widening forming a lorica-like thecostyle the species *P. multitentaculata* must be transferred into the genus *Pelagacineta* Jankowski, 1978. Respectively, the name *Pseudocorynophrya* Small et Lynn, 1985 is a younger synonym of *Pelagacineta* Jankowski, 1978.

#### GENUS *THALASSACINETA* JANKOWSKI, 1981

The genus *Thalassacineta* was elevated by A.V. Jankowski (1981) on the basis of arrangement of the tentacles in two lateral fascicles and a ribbon-like shape of macronucleus. Thereupon the type species of the genus (*Acineta euchaetae* Sewell, 1951) has been transferred by C. Curds (1987) into the genus *Pelagacineta*. Our investigations of the type species of A.V. Jankowski's genus (I.V. Dovgal, unpubl. data) show that *T. euchaetae* possesses a usual lorica, two apical groups of tentacles and endogemmic reproduction with the formation of a single bud. This is characteristic for the genus *Acineta*. Consequently, the name *Thalassacineta*

Jankowski, 1981 is a younger synonym of *Acineta* Ehrenberg, 1834.

**THE SYSTEMATIC POSITION OF *PODOPHYRYA MARINA*  
ANDRUSOVA, 1886**

*Podophrya marina* Andrusova, 1886 was indicated by A. Kahl (1934) as a type species of the genus *Corynophrya* Kahl, 1934 (with internal budding). In contrast, C. Curds (1987) believed that the “anterior notch in the body” of the species indicates invaginative budding. Consequently, *P. marina* must be transferred to an appropriate genus. In our opinion, the data available are insufficient for establishment of the mode of reproduction (the species diagnosis and figure Yu.I. Andrusova (1886) made from one individual). However, *P. marina* differs from other corynophryids by the presence of numerous and very agile tentacles (Fig. 25, H). On the strength of this we propose to establish for this species a new genus *Andrusovia* gen. n. Generic name is given in honour of Dr. Yu.I. Andrusova who is the author of the type species.

**GENUS *ANDRUSOVIA* DOVGAL, GEN. N.**

Marine suctorians with stalked sack-like body. The macronucleus is elliptical. Numerous capitate agile tentacles are distributed all over the cell body. The mode of reproduction is unknown. Type species: *Podophrya marina* Andrusova, 1886 (Fig. 25, H).

**GENUS *CAPRINIANA* STRAND, 1928**

Several species parasitizing on the gills of freshwater fishes and having not a “star-shaped body” were classified by A.V. Jankowski (1967a) in a separate genus *Phagobranchium* Jankowski, 1967. Subsequently this author (Jankowski, 1981) recognized that the genus *Caprina* Mazzarelli, 1906 with a similar diagnosis had been described earlier but the generic name was substituted (Strand, 1928) for *Capriniana* in connection with homonymy. The type species of the genus is *Trichophrya piscium* Bütschli, 1889 (Fig 26, D). The genus *Capriniana* was accepted by several investigators (Dovgal, 1988, 1991; Titar, 1989). However, typical characters by which the representatives of *Capriniana* differ from *Trichophrya* species cannot be seen with the help of the light microscopy. Based on this we (Dovgal, 1996) discussed the species from fishes as the representatives of the genus *Trichophrya*. Electron microscopy has disclosed that *T. piscium* attached to the host gill by characteristic adhesive tentacles (Batisse, 1994). In our opinion, this morphological adaptation could be sufficient for accepting of Strand’s genus.

**THE SYSTEMATIC POSITION OF *ERASTOPHYRYA WUCHANGENSIS*  
CHEN, 1964**

*Erastophrya wuchangensis* (Fig. 27, E) is an inhabitant of peritrichous ciliates *Apiosoma* sp. from Chinese freshwater fishes (Chen, 1964, cited after Matthes et al., 1988). The presence of 2-5 fascicles of tentacles, a stretched macronucleus and the attachment to the apiosoma’s stalk-like body protuberance by an adhesive ring (cinctum) are characteristic for the species. However, the cinctum of the species is formed not by two cell protuberances as in the type species *Erastophrya chattoni* Faure-Fremiet (Fig. 27, D) but by a single protuberance only. For this adhesive structure the term “hemicinctum” was proposed in chapter 2. *E. wuchangensis* differs from the type species of the genus *Erastophrya* by several important characters such as adhesive organelle morphology, arrangement of the tentacles in fascicles and the shape of macronucleus. Therefore we propose to classify *E. wuchangensis* into a new genus *Chenophrya* gen. n. Generic name refers to Dr. Chen that is the author of the type species.

**GENUS *CHENOPHYRYA* DOVGAL, GEN. N.**

Freshwater suctorians with an elongated body. The tentacles are arranged in several fascicles, actinophores are absent. The macronucleus is ribbon-like and extended along the body. The attachment to the host (apiosome peritrichs) body is effected by a special adhesive ring (hemicinctum). From the representatives of a related genus *Erastophrya* the new genus differs by arrangement of the tentacles in fascicles (and not all over the cell body), the morphology of macronucleus and adhesive organelle. Type species: *Erastophrya wuchangensis* Chen, 1964 (Fig. 27, E).

**THE SYSTEMATIC POSITION OF THE GENUS *BRACHIOSOMA*  
BATISSE, 1975**

The substituting name *Brachiosoma* was proposed by A. Batisse (1975) for *Hallesia* Sand, 1899 in connection with homonymy declared by J. Corliss (1960). In turn, the genus *Hallesia* was erected for endogemmie suctorians that lack both stalk and lorica and attach to the substrate by a basal cell protuberance. As the type species *Podophrya brachypoda* Stokes, 1885 (Fig. 26, C) was indicated. It is the opinion of A. Batisse (1975) that the genus must be assigned to the family Tokophryidae. C. Curds (1985c) also discussed the genus as relative to *Tokophrya*. However, lack of the stalk is characteristic for trichophryids and not tokophryids. Therefore we are transferring the genus *Brachiosoma*

Batiste, 1975 into the order Trichophryida Jankowski, 1978 and the family Trichophryidae Bütschli, 1879.

#### GENUS *GAJEWSKAJOPHRYA* MATTHES, 1988

The new genus *Gajewskajophrya* was erected (Matthes et al., 1988) with the following diagnosis: The body in form of polyhedron. Reproduction by binary fission. Swimmers probably are absent. Tentacles are arranged in fascicles. The stalk is absent. Type species: *Sphaerophrya melosirae* Gajewskaja, 1933.

The genus was classified into the family Podophryidae Bütschli, 1889.

*S. melosirae* leads the sessile mode of life on the water plants in lake Baikal. As C. Curds (1986) noted, reproduction by monotomy or by "pseudo-scissiparity" has not been adequately explored and calls for further investigation. According to its morphological features the species must be transferred into the genus *Trichophrya*. The name *Gajewskajophrya* Matthes, 1988 is synonymized with *Trichophrya* Claparede et Lachmann, 1859.

#### GENUS *ACTINOBRANCHIUM* JANKOWSKI, 1967

In the opinion of A.V. Jankowski (1981) the presence of characteristic tentacles lacking a knob is the main character of the genus *Actinobanchium* Jankowski, 1967. The type species of the genus is *Trichophrya salparum* Entz, 1884. However, there is a knob in the representatives of the genus, though flat, not spherical. As observed in the literature (see Foissner et al., 1995) and in our investigation a flat knob of the clavate tentacle is a common characteristic of various not related suctorian species. Consequently, the character is not generic. The name *Actinobanchium* Jankowski, 1967 is a younger synonym of *Trichophrya* Claparede et Lachmann, 1859.

#### GENUS *BAIKALOPHRYA* SWARCZEWSKY, 1928

The new genus *Baikalophrya* was described by B. Swarczewsky (1928a) for Baikalian dendrosomids with a flattened body sprawled along substrate with several actinophores around the periphery. *Baikalophrya acanthogammari* Swarczewsky, 1928, *B. digitata* Swarczewsky, 1928 and *B. lobata* Swarczewsky, 1928 were listed as the representatives of the genus but the type species was not indicated.

It is pertinent to note that the species listed above closely resemble the type species of the genus *Dendrosoma* Ehrenberg, 1838 (*D. radians*). Our data (Dovgal, 1996) show that a high variability of the type of substrate is characteristic for the latter. *D. radians* can be raised

when attached to the legs of water insects or crustaceans or flattened (indistinguishable from representatives of *Baikalophrya*) on flat surfaces. We believe that the same cases of intraspecific variability are possible both in European and Baikalian habitats. The generic name *Baikalophrya* Swarczewsky, 1928 is synonymized with *Dendrosoma* Ehrenberg, 1838, and the species names *Baikalophrya acanthogammari* Swarczewsky, 1928, *B. digitata* Swarczewsky, 1928 and *B. lobata* Swarczewsky, 1928 are synonymized with *Dendrosoma radians* Ehrenberg, 1838.

#### GENUS *BAIKALODENDRON* SWARCZEWSKY, 1928

B. Swarczewsky (1928a) considered the presence of several elevated ramified actinophores as the key character of the genus *Baikalodendron*. The type species of the genus (by monotypy) is *Baikalodendron augustatum* Swarczewsky, 1928 from lake Baikal. B. Swarczewsky has stated that *Baikalodendron* is related to the genus *Dendrosoma*, since the representatives of the latter also have elevated actinophores. In such a case, ramification of actinophores is the sole distinction between the genera.

However, B. Swarczewsky made no mention of the fact that there were both branched and non-ramified actinophores in *D. radians* (for example, see Foissner et al., 1995; Dovgal, 1996). Consequently, these differences are the cases of intraspecific variability and cannot be used as generic characters. The name *Baikalodendron* Swarczewsky, 1928 is a younger synonym of *Dendrosoma* Ehrenberg, 1838 and the specific name *Baikalodendron augustatum* Swarczewsky, 1928 is a younger synonym of *Dendrosoma radians* Ehrenberg, 1838.

#### GENUS *LERNAEOPHRYA* PEREZ, 1903

The genus *Lernaeophrya* was described from brackish-water hydroids (Perez, 1903). The type species is *Lernaeophrya capitata* Perez, 1903. The presence of numerous short actinophores (to distinguish from long in *Dendrosoma*) is the key character of the genus.

However, the representatives of *Dendrosoma* may have both long and short flattened actinophores. Thus such characteristic as actinophores length cannot be used as generic. But the presence of numerous (more than 12) actinophores is characteristic of *L. capitata* whereas 10 actinophores are characteristic of *D. radians*. It seems plausible that Perez's species is a separate brackish-water species of the genus *Dendrosoma*. Consequently, we synonymize the name *Lernaeophrya* Perez, 1903 with *Dendrosoma* Ehrenberg, 1838 and transfer *L. capitata* Perez, 1903 into the latter genus.

**GENUS *VENODISCPHRYA* JANKOWSKI, 1981**

The new genus *Venodiscophrya* was proposed by A.V. Jankowski (1981) for discophryins with the tentacles that are not arranged in fascicles and with unramified macronucleus. The type species of the genus is *Podophrya lichtensteinii* Claparede et Lachmann, 1859. The genus was accepted by A. Batisse (1994). However, in discophryin suctorians it is often difficult to estimate whether or not tentacles are arranged in fascicles. Both interspecific and intraspecific variability of this character exists. Thus, the arrangement of tentacles is not a generic character in discophryids. The shape of macronucleus in *P. lichtensteinii* is the same as in other representatives of the genus *Discophrya* Lachmann, 1859. Respectively, the name *Venodiscophrya* Jankowski, 1981 is a younger synonym of *Discophrya* Lachmann, 1859.

**GENUS *FERODISCPHRYA* JANKOWSKI, 1981**

The genus *Ferodiscophrya* was elevated by A.V. Jankowski (1981) for discophryins with tentacles that are not arranged in fascicles and with a horseshoe-like macronucleus. The type species is *Acineta cothurnata* Weisse, 1847. As discussed above, the arrangement of tentacles is an inapplicable generic character in discophryids. It is also difficult to discriminate between a horseshoe-like macronucleus and an elongated one. The name *Ferodiscophrya* Jankowski, 1981 must be synonymized with *Discophrya* Lachmann, 1859.

**GENUS *CORONODISCPHRYA* JANKOWSKI, 1981**

A.V. Jankowski (1981) proposed the genus *Coronodiscophrya* for the discophryin species with an unflattened body and tentacles that are placed both on the apical and basal body surfaces. The type species of the genus is *Discophrya prismatica* Holm, 1925. The arrangement of the tentacles is not a generic character, and the same is true for the body shape. The name *Coronodiscophrya* Jankowski, 1981 is a younger synonym of *Discophrya* Lachmann, 1859.

**GENUS *EPIDISCPHRYA* JANKOWSKI, 1981**

The genus *Epidiscophrya* was erected by A.V. Jankowski (1981) for discophryid suctorians with a shallow wine-glass-like lorica. The type species of the genus is *Discophrya elongata* var. *scyphostyla* Collin, 1911. This genus was accepted by A. Batisse (1994). In fact, the species that were assigned to this genus have an apical widening of the stalk rather than semilorica. This character is widespread in discophryids and is

inapplicable as a generic one. The name *Epidiscophrya* Jankowski, 1981 is a younger synonym of *Discophrya* Lachmann, 1859.

**GENUS *PARADISCPHRYA* JANKOWSKI, 1981**

The genus *Paradiscophrya* was erected by A.V. Jankowski (1981) for discophryins with an unflattened body and with tentacles located as in *Coronodiscophrya* but not arranged in circular groups. The type species is *Podophrya astaci* Claparede et Lachmann, 1858. The genus was also accepted by A. Batisse (1994). In our opinion, arrangement of tentacles and body shape are not generic characters. The name *Paradiscophrya* Jankowski, 1981 is synonymized with *Discophrya* Lachmann, 1859.

**GENUS *CYATHODISCPHRYA* JANKOWSKI, 1978**

The genus was erected by A.V. Jankowski (1978) for discophryins with semilorica. The *Discophrya cyathostyla* Matthes, 1954 was indicated as the type species. As noted above we do not accept the presence of a cup-like stalk widening as a generic character. The name *Cyathodiscophrya* Jankowski, 1978 is a younger synonym of *Discophrya* Lachmann, 1859.

**GENUS *MESODISCPHRYA* JANKOWSKI, 1981**

Several discophryan species with a ramified macronucleus (as in *Setodiscophrya* Jankowski, 1981) but with tentacles that are not arranged in clearly defined fascicles were classified by A.V. Jankowski (1981) into a separate genus *Mesodiscophrya*. The type species of the genus is *Podophrya steinii* Claparede et Lachmann, 1858. The genus was accepted by A. Batisse (1994). However, tentacle arrangement is not a generic character in discophryins. We synonymize the name *Mesodiscophrya* Jankowski, 1981 with *Setodiscophrya* Jankowski, 1981. The species *Mesodiscophrya steinii* (Claparede et Lachmann, 1858), *M. operculariae* (Stein, 1859) and *M. setarcon* Jankowski, 1981 are transferred into *Setodiscophrya*. The species *M. erlangensis* (Matthes, 1954) and *M. deplanata* (Matthes, 1954) have already been transferred into this genus (Dovgal, 1996).

**THE PROBLEM OF THE GENERIC NAME *PERIDISCPHRYA***

A new suctorian genus was independently described under the same name *Peridiscophrya* (but with a different species composition) by J. Kormos (1938b) and K. Nozawa (1938).

The suctorian with cylindrical or finger-like body totally covered by stylothea belongs to K. Nozawa's

genus. The length of a stalk-like protuberance of the lorica does not exceed one third of the total body length. Capitulate tentacles are arranged in a single apical fascicle. The macronucleus is ramified. There are numerous (not less than 4) contractile vacuoles. The type species of the genus (Jankowski, 1981) is *P. japonica* Nozawa, 1938 (Fig. 28, H) from the shells of freshwater molluscs *Viviparus* sp. The species *Podophrya cylindrica* Perty, 1852 and *Discophrya robusta* Nozawa, 1938 were transferred by A.V. Jankowski (1981) into K. Nozawa's genus.

A.V. Jankowski (1981) thought that suctorians with triangular, laterally flattened body covered with a stylothea with a very short stalk-like protuberance belong to J. Kormos' genus. Clavate tentacles are arranged in two apical fascicles. *Acineta linguifera* Claparede et Lachmann, 1858 (Fig. 28, F) was indicated as the type species of J. Kormos' genus by A.V. Jankowski (1981) without any comments on the way of its fixation but possibly as first mentioned on p. 13 of J. Kormos' monograph.

Attempts to establish whose generic name (J. Kormos' or K. Nozawa's) was published earlier have so far been unsuccessful. A.V. Jankowski (1981) was the pioneer ciliatologist to call attention to this nomenclature problem. A.V. Jankowski (1981) suggested that J. Kormos had probably used the name *Peridiscophrya* independently from K. Nozawa but without indication "gen. n.". We (Dovgal, 1988, 1991, 1996) previously used J. Kormos' generic name.

K. Nozawa's work (1938) was issued on November 18, but our attempts to establish the exact date of J. Kormos' publication were unsuccessful. However, J. Kormos did not indicate the type species of the genus. He used (without indication of the authors) two specific names: "*buckei*" (*Podophrya buckei* Kent, 1882) and "*linguifera*" (*Acineta linguifera* Claparede et Lachmann) in combination with the generic name *Peridiscophrya*. This renders the fixation of the type species by monotypy impossible. It should be also noted that there is no stylothea in the species *Peridiscophrya buckei*.

However, a generic name published after 1931 is unsuitable if not accompanied by fixation of a type species (International Code of Zoological Nomenclature, 2000). This is the case with the name *Peridiscophrya* Kormos, 1938. Consequently we believe that *Peridiscophrya* Nozawa, 1938 must be conserved as a valid name. The type species of the genus (by monotypy) is *P. japonica* Nozawa, 1938. We eliminated *Podophrya cylindrica* and *Discophrya robusta* from the genus because of the lack of the stylothea in these species.

However, in our view the species of discophryid suctorians that are characterized by a laterally flattened body with two fascicles of tentacles and the stylothea

must be separated from related forms with an ordinary lorica. Therefore we propose a new genus *Kormosia* gen. n. for these species. Generic name is given in honour of a famous Hungarian protozoologist Dr. J. Kormos.

#### GENUS *KORMOSIA* DOVGAL, GEN. N.

Freshwater loricate discophryid suctorians with a laterally flattened body and capitulate tentacles arranged in two apical fascicles. The lorica (stylothea) is attached to the substrate by a short stalk-like protuberance. The macronucleus is spherical or elliptical. Type species: *Acineta linguifera* Claparede et Lachmann, 1859 (Fig. 28, F).

#### GENUS *CARACATHARINA* KORMOS, 1968

The substituting name *Caracatharina* was proposed instead of the generic name *Catharina* Kormos, 1957 in connection with assumed homonymy of the latter. The type species of the genus is *Catharina florea* Kormos, 1957. A.V. Jankowski (1981) has established that the name *Catharina* is not a homonym and *Caracatharina* was indicated as the younger synonym of *Catharina*. However, the coincidence of the diagnoses of the genera *Peridiscophrya* Nozawa, 1938 and *Catharina* Kormos, 1957 escaped the attention of this author. In fact, the presence of apical fascicle of tentacles, a ramified or ribbon-like macronucleus and the stylothea is characteristic for both Nozawa's and Kormos' genera. Consequently, the names *Catharina* Kormos, 1957 and *Caracatharina* Kormos, 1968 are the younger synonyms of *Peridiscophrya* Nozawa, 1938. The species *Catharina florea* Kormos, 1957 must be transferred into the genus *Peridiscophrya*.

#### GENUS *ANISARCON* JANKOWSKI, 1981

The substituting name *Anisarcon* was proposed for *Calix* Fraipont, 1878 (in connection with homonymy) by A.V. Jankowski. The genus included periacinetid suctorians with an asymmetrical lorica. The *Acineta notonectae* Claparede et Lachmann, 1858 was indicated as the type species. However, we do not accept the shape of the lorica as a generic character. Therefore we synonymize the name *Anisarcon* Jankowski, 1981 with *Periacineta* Collin, 1909. The species *Acineta notonectae* was previously transferred into the genus *Periacineta* (Dovgal, 1988, 1991).

#### GENUS *ARCODISCOPHYA* JANKOWSKI, 1981

The new genus *Arcodiscophrya* was described by A.V. Jankowski (1981) for periacinetid suctorians with

an allometric growth of the aperture of the lorica. The type species of the genus is *Arcodiscophrya heraldica* Jankowski, 1981 (the species name was in turn proposed for “Gelenkform von *Discophrya hydrochi*” in Matthes, 1954a, Fig. 19, p. 209). As discussed above, the outlook of the lorica is not a generic character. The name *Arcodiscophrya* Jankowski, 1981 must be synonymized with *Periacineta* Collin, 1909. The species *A. heraldica* is transferred into the genus *Periacineta*.

#### GENUS *TOMODISCOPHRYA* JANKOWSKI, 1981.

A.V. Jankowski (1981) proposed to classify discophryid suctorians with trophont morphology characteristic of *Periacineta* but with swarmer similar to representatives of *Silenella* Fenchel, 1965 in a separate genus *Tomodiscophrya*. *Acineta paratuberosa* Nie et Ho, 1943 was indicated as the type species. However, in the same article A.V. Jankowski suggested that representatives of *Silenella* closely resemble discophryid swarmer. In such an event, the swarmer of *A. paratuberosa* are morphologically similar to the swarmer of other discophryid species. Thus, there are no reasons to classify *A. paratuberosa* in a separate genus. The name *Tomodiscophrya* Jankowski, 1981 is a younger synonym of *Periacineta* Collin, 1909 and the species *A. paratuberosa* must be transferred into the genus *Periacineta*.

#### THE SYSTEMATIC POSITION OF *TRICHOPHRYA ROTUNDA* HENTSEL, 1916

*Trichophrya rotunda* (Fig. 28, J) is the type species of the genus *Heliophrya* De Saedeleer et Tellier, 1930 (Matthes, 1954d; Jankowski, 1981; Rieder, 1988; Dovgal, 1996). More recently Mogensen and Butler (1984) investigated the ultrastructure and reproduction of this species. In the opinion of these authors, *T. rotunda* is closer to suctorians with endogemmy than with inversogemmy according to its ultrastructural characters. In particular, the species differs in some ultrastructural details from another representative of the genus – *H. erhardi* (Rieder, 1936). On the basis of these data *T. rotunda* was retransferred from the genus *Heliophrya* to the genus *Trichophrya*. Other authors (Matthes et al., 1988; Rieder, 1988; Batisse, 1994; Foissner et al., 1995; Dovgal, 1996) classified the species as a representative of *Heliophrya*. However, A. Batisse (1994) assigned the latter genus to the family Trichophryidae (with internal budding) and not to Discophryidae Collin, 1912 where the related species from the genus *Cyclophrya* were indicated.

We emphasize that Mogensen and Butler (1984) ignored the fact that *H. erhardi* was a younger synonym of the type species of the genus *Cyclophrya* (*Cyclophrya*

*magna* Gonnert, 1935 (Fig. 28, K) has a ramified macronucleus, whereas representatives of *Heliophrya* possess a spheroid or ellipsoid macronucleus). Thus it is not surprising that the representatives of different genera demonstrate ultrastructural differences. In addition, it is clear from Fig. 1 of Mogensen's and Butler's article that these authors investigated at least two species, because *Heliophrya minima* (Rieder, 1936) is shown at the photograph mentioned. However, A. Batisse and some other authors did not take into account the principal point that in the article of Mogensen and Butler (1984) typical inversogemmy was described in representatives of *Heliophrya*. The same mode of reproduction was observed both in *H. rotunda* and *H. minima* in the course of our investigations. In our view, it is unreasonable to remove *T. rotunda* from *Evaginogenia* Jankowski, 1978. The combination *Heliophrya rotunda* (Hentshel, 1916) is conserved for the species.

#### GENUS *PARAHELIOPHRYA* JANKOWSKI, 1978

The new genus *Paraheliophrya* was erected by A.V. Jankowski (1978) for heliophryin suctorians with tentacles that are not arranged in fascicles. The type species of the genus is *Craspedophrya rotunda f. minima* Rieder, 1936. However, we do not accept the arrangement of tentacles as a generic character in Heliophryidae Corliss, 1979. Consequently, the name *Paraheliophrya* Jankowski, 1978 is a younger synonym of *Heliophrya* De Saedeleer et Tellier, 1930.

#### THE SYSTEMATIC POSITION OF THE GENUS *DISCOSOMATELLA* CORLISS, 1960

The substituting name *Discosomatella* was proposed by J. Corliss (1960) instead of a homonym name *Discosoma* Swarczewsky, 1928. The type species is *D. tenella* Swarczewsky, 1928 (Fig. 29, D) from Baikalian gammarid amphipods (Swarzewsky, 1928b). The body of the type species is flattened and disc-like with several rows of the rod-like tentacles at the apical surface. The macronucleus is ellipsoid. In the body shape this species is similar to representatives of the genus *Heliophrya* but differs from them by the shape of the tentacles that are not capitate. In our opinion, the type of tentacles and body outlooks attest to the affinity of this species with the genus *Stylocometes*. For this reason the genus is transferred into the family Stylocometidae Jankowski, 1981.

#### THE SYSTEMATIC POSITION OF *CHOANOPHRYA STENASELLI* MATJASIC, 1963

The new suctorian species *Choanophrya stenaseilli* was described by J. Matjasic (1963) from Jugoslavian

cave-dwelling isopodes. The mode of reproduction is unknown. The representatives of the species are stalked, with spherical body and ellipsoid macronucleus. From the figures of J. Matjasic's article it is clear that the tentacles are not funnel-like (as in *Choanophrya* Hartog, 1901) (Fig. 25, L) but rod-like. D. Matthes and others (1988) transferred the species into the genus *Stylocometes* on the basis of the latter character. However, the stalk is lacking in *Stylocometes*. In our opinion, the species of J. Matjasic is similar to *Echinophrya horrida* Swarczewsky, 1928 (Fig. 29, C) from Baikalian gammarids (Swarzewsky, 1928c). Therefore we transfer the species *C. stenaselli* Matjasic into the genus *Echinophrya* Swarczewsky, 1928.

#### GENUS *DENDROCOMETIDES* SWARCZEWSKY, 1928

The genus *Dendrocometides* was elevated by B. Swarczewsky (1928b). The type species of the genus is *D. priscus* Swarczewsky, 1928 from Baikalian gammarid amphipodes. Hemispherical body, ellipsoid macronucleus and ramified tentacles are characteristic for the genus. As to these characters, *D. priscus* is similar to representatives of the genus *Dendrocometes*, differing only by pointed tentacle ends. The ultrastructure of the tentacles has not been investigated to date. It is our opinion that a larger diameter of the terminate parts of

tentacles is not sufficient for delimiting a new tentacle type. Thus, there is no reason to erect a separate genus. We synonymize the name *Dendrocometides* Swarczewsky, 1928 with *Dendrocometes* Stein, 1851 and transfer the type species into the latter genus.

#### GENUS *SILENELLA* FENCHEL, 1965

A new monotypical genus *Silenella* was described by T. Fenchel (1965) from gills and pereopods of brackish-water gammarid amphipods. The type species is *Silenella ovoidea* Fenchel, 1965. The presence of a ribbon-like macronucleus, reduced somatic ciliature and lack of the cytostome are characteristic for the genus. The systematic position of *Silenella* in the phylum Ciliophora remains obscure. T. Fenchel (1965) presumed that *S. ovoidea* is similar in some details to suctorian swimmers. A.V. Jankowski (1981) included the genus in Suctorea as possibly related to periacinetid suctorians and indicated that the type species closely resembles discophryid swimmers. In our view, these organisms is similar not only to suctorian swimmers but also to apostomates, pilisuctorids, etc. The data currently available on the genus are probably insufficient to classify it into any ciliated taxon, including Suctorea.

## CHAPTER 4. THE PHYLOGENY OF SUCTOREA

It has already been said that there are several versions of the suctorian system based on different estimations of the characters' values.

For example, the mode of budding is accepted by many authors as a common character defining suctorian taxa of the highest rank. However, in the system of A.V. Jankowski (1980) this rank is subclass, in that of A. Batisse (1994), the order, and in that of D. Matthes and others (1988), suborder. Aside from taxonomical rank there is no agreement among the specialists regarding the number of budding modes. A.V. Jankowski (1981) recognized four modes, D. Matthes and others (1988) only three, and A. Batisse (1994) up to seven.

As for morphological characters, the disagreements are more sophisticated. In the opinion of D. Matthes' (Matthes and Guhl, 1975), the system of ciliates must be based mostly on non-adaptive characters, such as morphology of the macronucleus. Following A.V. Jankowski's (1981) concept, the genera of suctorians must include only morphologically similar species, but any species deflecting from the type species must be classified into a separate subgenus or genus. These

differences often concern a single character only. Hence numerous monotypical genera were erected by A.V. Jankowski (see above).

The considerations of both D. Matthes and A.V. Jankowski are not unreasonable. Yet it is impossible to solve the contradictions in Suctorea systematics without invoking new data, mostly on phylogenetic relations of suctorian taxa. However, no concepts concerning suctorian phylogeny have been discussed in systematic papers in the last two decades.

In our opinion, it is interesting to estimate phylogenetical relations in Suctorea with Hennigian approach.

The cladistic approach has the advantage that the totality of characters are analyzed regardless of the rank of taxa, whereas in classic methods the number of characters tends to decrease depending on the taxonomical rank (Jenner and Schram, 1999). This is particularly important in the absence of palaeontological data as in Suctorea.

In the course of preparing of the matrixes of suctorian characters we followed the recommendations



of R. Jenner and F.R. Schram (1999). The evaluation of characters and their states was conducted on the basis of our concept of suctorian evolution discussed above.

### Mode of reproduction and traits of the life cycle

In our view the formation of different modes of budding provides the basis for the initial divergence in suctorians. Therefore the type of budding is a conservative character and reliably testifies to the affinity between taxa. However, in the context of the presence of binary fission in several suctorian groups it is more correct to speak about the mode of reproduction than about the manner of budding. Several suctorian species retain binary fission with exogemmy but some parasites and commensals of mammalian intestine probably lost budding secondarily. Thus, we use the monotomy as a character of a similar rank with budding mode.

The following modes of reproduction are used as the possible states of the character “mode of budding”: exogemmy, semi-circumvaginate budding, vermigemmy, endogemmy and inversogemmy.

We are the first to use protomit position as a reproduction character. This character has two states: apical and lateral locality.

Mode of conjugation with mobile microconjugants has been previously discussed before as a generic character in suctorians (Kormos, 1935a). However, in various suctorian taxa the transition from isogamy to anisogamy may occur and this character is quite suitable if a totality of characters is used.

### Swarmer morphology

As may be inferred from the literature (Batisse, 1994), the similar swarmer morphotypes are independently formed in unrelated suctorian groups, for example in ephelotid and discophryid or in podophryid and enchelyomorphid suctorians. However, parallelism in tomit morphology is unknown within suctorian groups classified by mode of budding. The similarity in the swarmer morphology is a manifestation of the principle of tomit similarity (Dovgal, 2002) and may reliably testify the affinity at this level.

### Morphology and function of the tentacle apparatus

The most important taxonomical characters are associated with morphology of tentacles. A.V. Jankowski (1981) considered no less than 15 types of tentacles. However, in our opinion characters based only on tentacle thickness and on knob development

or shape cannot be used to distinguish a tentacle type. For example, A.V. Jankowski (1981) discriminated nail-like and capitate tentacles but the differences might be indistinguishable with light microscopy. According to our observations, regular clavate tentacles of discophryid suctorians *Periacineta buckei* (Kent, 1882) and *Discophrya elongata* (Claparede et Lachmann, 1859) in fact bear a spherical knob in the former and a flat one (nail-like) in the latter (Fig. 12). Therefore we considered only the following types of tentacles as applicable states of the character “type of tentacle”: capitate, rod-like, ramified, funnel-like and endosprits. Additional prehensile organelles of ephelotid suctorians were considered as a separate apomorphic character.

The characters based on morphology and function of tentacles of different modes (feeding, attachment) and their number (in case of partial oligomerization, when from 1 to 3 tentacles are present) were also used. The features of actinophore morphology were also applied.

### The morphology of adhesive organelles

The mode of adhesive organelles is also discussed in taxonomical works (see Jankowski, 1981; Matthes et al., 1988; Dovgal, 1996). We considered the presence of the stalk and adhesive disk, attachment by body surface, body protuberance or cinctum as taxonomic characters. A.V. Jankowski (1973b) also distinguished the stalk and pedicle. In his opinion the stalk is different from the pedicle in proportion. The stalk diameter is less than its length, whereas the diameter of pedicle is equal or exceeds the length. Therefore the differentiation between stalk and pedicle amounts to the degree of character development. Thus, in contrast to A.V. Jankowski we do not accept the pedicle as a character.

### The morphology of lorica

Taxonomical significance of this structure was a matter of contention between D. Matthes and A.V. Jankowski. Following A.V. Jankowski, we used the type of lorica (regular, stylothea, mucous, but except semilorica) as a group of generic characters though various modes may develop in several genera of one family in parallel. Particularly it concerns mucous lorica forming at the expense of the glycocalyx amplification only.

### Macronucleus morphology

Macronucleus morphology is also an important character already in use (Jankowski, 1981; Dovgal,

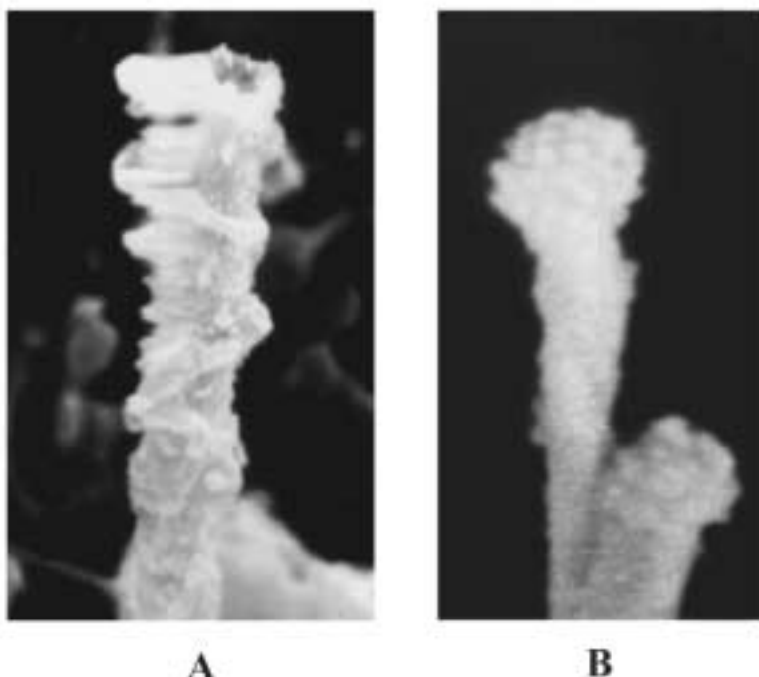


Fig. 12. The knob morphology of (A) *Discophrya elongata* (Claparede et Lachmann, 1859) (SEM, x8600) and (B) tentacles of *Periacineta buckei* (Kent, 1882) (SEM, x15000).

1996). However, D. Matthes and others (1988) do not apply this “inadaptive” character to distinction of genera in Suctorea, though they do so in Peritrichia Stein, 1859.

We believe that inadaptivity of the macronucleus shape deserves further comments. As discussed above, progressive evolution of sessile protists is associated with the increase of body size. However, the size of nucleus correlates with cell dimensions. Thus, the tendency may be followed in suctorians from lengthening of initial spherical macronucleus to its ramification. Consequently, the amplification of the function of vegetative nucleus is associated with adaptive changes in size and shape of the body. Adaptivity of the ramified macronucleus is particularly striking in ephelotid suctorians. As mentioned above, the axonemae of their prehensile tentacles begin from special invaginations in macronucleus protrusions (Mikrjukov, 1997). The branches of macronucleus perform the mechanical function (Dovgal, 2000). Thus, in contrast to German authors (Guhl, 1979), the morphology of macronucleus is also an “adaptive” character. However, macronucleus morphology may be applied for phylogenetic interpretations.

### The shape of body and arrangement of the tentacles

This large group of the characters is customarily used for distinguishing lower suctorian taxa. However, most cases of homoplasy were associated with these characters. Therefore this group was eliminated from the character matrices.

The groups of characters associated with reproduction and life cycle, feeding apparatus, adhesive organelles and derivative from these structures (tectinous loricas) may be used for analysis of suctorian phylogenetic relations.

Characters associated with reproduction and morphology that are used in suctorian taxonomy and their states are summarised in the following list:

1. Reproduction by binary fission (monotomy): 0 - yes; 1 - no; ? - unknown state.
2. Mode of budding: 0 - exogemmic; 1 - semi-circumvaginate exogemmic budding; 2 - vermigemmic budding; 3 - endogemmic budding; 4 - inversogemmic budding; 5 - the state absent; ? - unknown state.
3. Protomit position: 0 - apical; 2 - lateral; 3 - the state absent; ? - unknown state.
4. Life cycle with alternation of generations: 0 - yes; 1 - no; ? - unknown state.
5. The mode of conjugation: 0 - isogamic; 1 - anisogamic involving trophonts; 2 - anisogamic involving trophont and mobile microconjugant; ? - unknown state.
6. The tentacles in protomit: 0 - yes; 1 - no; ? - unknown state.
7. The anlagen of the tentacles in protomit: 0 - yes; 1 - no; ? - unknown state.
8. Swarmer ciliature: 0 - yes; 1 - no; ? - unknown state.
9. Perforatorium: 0 - yes; 1 - no; ? - unknown state.

10. The presence of the tentacles: 0 - yes; 1 - no; ? - unknown state.
11. The tentacle type: 0 - capitate; 1 - rod-like; 3 - endosprits; 4 - funnel-like; 5 - ramified; 6 - absent; ? - unknown state.
12. The morphology and function of capitate tentacles: 0 - regular; 1 - with basal widening; 2 - flexible; 3 - prehensile with reduced axonema; 4 - finger-like; 5 - no; ? - unknown state.
13. The morphology and function of rod-like tentacles: 0 - feeding; 1 - attachment; 2 - feeding and attachment; 3 - no; ? - unknown state.
14. The function of ramified tentacles: 0 - feeding; 1 - attachment; 2 - no; ? - unknown state.
15. Additional prehensile organelle: 0 - absent; 1 - present; ? - unknown state.
16. Numbers of tentacles: 0 - more than two; 1 - two tentacles; 2 - single tentacle; 3 - no; ? - unknown state.
17. Actinophore: 0 - yes; 1 - no.
18. The degree of actinophore development: 0 - slightly developed; 1 - well-developed body protuberances; 2 - absent; ? - unknown state.
19. Actinophore morphology: 0 - unramified; 1 - ramified; 2 - «proboscis-like»; 3 - no; ? - unknown state.
20. Attachment: 0 - yes; 1 - no.
21. The mode of attachment: 0 - by body surface; 1 - by stalk; 2 - by stalk-like protuberance of the stylotheca; 3 - by tentacle; 4 - by cinctum; 5 - absent.
22. The attachment by body surface: 0 - by basal surface; 1 - by body protuberance; 2 - no.
23. Stalk morphology: 0 - tectinous adhesive disk; 1 - regular stalk; 2 - polymerization of the stalk; 3 - no.
24. The morphology of stalk protuberance: 0 - slightly expanded; 1 - cup-like expanded; 2 - endostyle; 3 - no.
25. Cinctum morphology: 0 - from two body protuberances; 1 - from single protuberance; 2 - no.
26. The presence of lorica: 0 - no; 1 - yes.
27. Regular lorica: 0 - yes; 1 - no.
28. The degree of regular lorica development: 0 developed; 1 - semilorica; 2 - no.
29. The morphology of regular lorica: 0 - symmetrical; 1 - asymmetrical; 2 - with thorns; 3 - ribbed; 4 - no.
30. The shape of regular lorica aperture: 0 - with even edge; 1 - slit-like; 3 - no.
31. Stylotheca: 0 - present; 1 - no.
32. The degree of stylotheca development: 0 - complete developed; 1 - semilorica; 2 - no.
33. The morphology of stylotheca: 0 - symmetrical; 1 - asymmetrical; 2 - with thorns; 3 - ribbed; 4 - no.
34. The shape of stylotheca aperture: 0 - with even edge; 1 - with cuts; 2 - slit-like; 3 - aperture absent; 4 - no.
35. Mucous lorica: 0 - yes; 1 - no.
36. The shape of macronucleus: 0 - spherical or ellipsoid; 1 - ribbon-like; 2 - ramified; ? - unknown state.

As illustrated in the cladogram given by J.L. Riley's and L.A. Katz's (2001) (based on rDNA data) that included suctorian species with various modes of budding (*Prodiscophrya solaris* (Stein, 1859) named *Prodiscophrya collini* (Root, 1915) by the authors, *Ephelota* sp. and *Cyclophrya magna* named *Heliophrya erhardi*) the Suctorea can be provisionally considered as monophyletic group. Based on the evolutionary tendencies discussed in Chapter 2 the following characters may be recognized as plesiomorphic: monotomy (character 1 with state 0, subsequently symbolised as "1.0"), lack of budding (2.5), lack of obligate attachment and attachment organelles (20.1), lack of the lorica (26.0), isogamy (5.0). In our view the hypothetical ancestor of the suctorians may have possessed of listed properties. Although, as noted above, we do not have enough reason to consider didiniid ciliates as ancestors of suctorians, didiniids possess nearly all features mentioned. Thus we used the genus *Didinium* as the outgroup in all analyses discussed below. The computations were performed using the schedule HENNIG 86.

It has already been mentioned that the formation of several modes of budding was the basic tendency in suctorian evolution. Morphological features including feeding apparatus most likely developed in parallel. Considering this, the phylogenetical relations in Suctorea were analyzed singly within the four groups with different reproduction modes. However, the relations between the mentioned groups were our initial concern. Only the first group of characters from the list were used in the process (Table 1).

As a result we obtained the parsimonious tree with length 8, consistency index (ci) that comprises 100 and retention index (ri) 100 (Fig. 13). Exogemmin suctorians were indicated as initial group that is brought with outgroup by ability to binary fission (character 1.0). Another three clusters are represented by suctorians that lost this feature (character 1.1). The outlines obtained accord well with the present views on both budding evolution and phylogeny of Suctorea (Kormos and Kormos, 1957; Jankowski, 1980; Dovgal, 1996). Within clusters obtained the character matrixes were made up

**Table 1.** States of characters in subordinate groups within Suctoria (explanation are in the list of characters).

Taxa	Characters				
	1	2	3	4	5
<i>Didinium</i> (outgroup)	0	?	2	1	0
Exogenia	0	0	?	0	0
Vermigenia	1	2	?	1	0
Endogenia	1	3	2	1	0
Evaginogenia	1	4	2	1	2

using characters of the type species of suctorian genera and the totality of features involved.

### Phylogenetic relations within exogemmins

The characters of type species from 31 genera were processed (Table 2). As a result we obtained about 100 trees with length 156, ci=48 and ri=78. The consensus cladogram (Fig. 14) contains two major groups of genera characterized by presence (31.0) or absence (31.1) of the stylothecca.

The genera *Phalacrocleptes*, *Manuelophrya* and *Ophryocephalus* positioned in the first cluster lack the lorica.

Reproduction by monotomy only (characters 1.0 and 2.5) bring together the genus *Phalacrocleptes* and the outgroup. In our opinion this is due to the specialization of the genus to ectoparasitism only. The position of the genus can be also attributed to adaptations associated with the change of tentacle function from feeding to adhesive. The position of the genus *Manuelophrya* can be explained in an analogous way. In other characteristics [semi-circumvaginate budding (2.1), lateral protomit position (3.1), rod-like tentacle (11.2)] the representatives of the genus are related to the loricate parasitic genera *Mistarcon* and *Pseudogemmidis*.

As for the genus *Ophryocephalus*, its position at the diagram is attributable to a single flexible tentacle

similar to that in representatives of the genus *Urnula*. However, some other characters such as simultaneous multiple budding show that the genus probably has affinity to *Ephelota* and related genera.

Unique life cycle with alternation of generations and formation of both ciliated and non-ciliated swimmers is characteristic of the genus *Tachyblaston* Martin, 1909. It is customary to position this genus near *Ephelota* it parasitizes on (Kahl, 1934). Yet according to such characters as stylothecca presence (at “dactylophrya stage”) and lateral protomit position *Tachyblaston* should be placed near metacinetid suctorians.

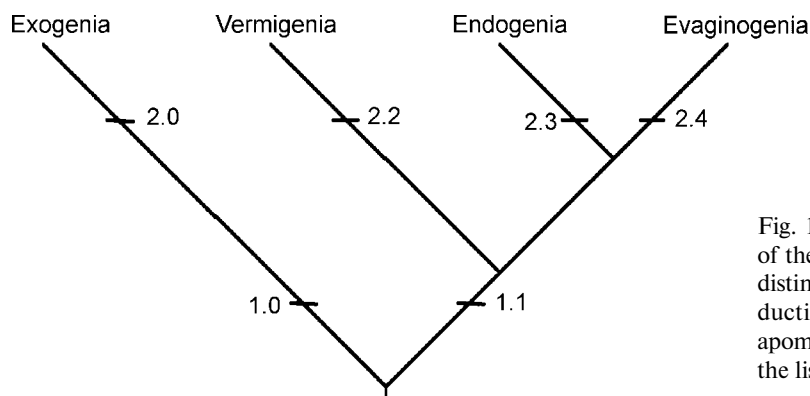
The loricate suctorians with stylothecca (31.0) make up a compact group within the first cluster.

In another cluster a set of genera differing in presence of additional prehensile organelles (*Ephelota* and relative genera) stand out. In our view the position of the genus *Praethecacineteta* Matthes, 1956 in the cluster is associated with homoplastic character, the presence of lorica. (Lorica is also characteristic of *Shellephelota* Jankowski, 1981 and (mucous lorica) of *Luxophrya* Jankowski, 1978).

On the whole, there are rather many cases of homoplasy within exogemmin suctorians as demonstrated by consistency index (48). However, if we eliminate the cases when the outlines are affected by parallelisms (position of *Praethecacineteta* and *Ophryocephalus*), the tree adequately reflects the phylogeny of suctorians with exogemmic budding.

Both evolutionary lineages that stand out begin from several primitive forms similar to podophryans.

Thus, we derive the ephelotin suctorians with additional prehensile structures and corona-like ramified macronucleus from podophryans. As discussed in Chapter 2, the prehensile tentacles of ephelotids formed independently of sucking ones. This suggestion is favoured by the fact that the microtubular pattern of axonema in the former differs markedly from that in the latter and also by the fact that regular haptocysts are present in prehensile tentacles (Mikrjukov, 1997).



**Fig. 13.** Phylogenetical relationships of the major groups within Suctorea distinguished by the mode of reproduction. The numbers of principal apomorphies correspond to those in the list of characters.

**Table 2.** States of the generic characters within Exogenia (explanation are in the list of characters).

Taxa	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Didinium</i> (outgroup)	0	5	2	1	0	1	1	1	1	1	6	5	3	2	0	3	1	2	3	1
<i>Parapodophrya</i>	0	1	0	1	0	0	1	1	1	0	0	1	3	2	0	0	1	2	3	0
<i>Podophrya</i>	1	1	0	1	0	0	1	1	1	1	1	0	3	2	0	0	1	2	3	0
<i>Sphaerophrya</i>	0	1	0	1	0	0	1	1	1	1	1	0	3	2	0	0	1	2	3	1
<i>Vanhovenia</i>	0	5	2	1	?	1	1	1	1	0	0	0	3	2	0	0	1	2	3	1
<i>Allantosoma</i>	0	5	2	1	?	1	1	1	1	0	0	0	3	2	0	0	1	2	3	1
<i>Arcosoma</i>	0	5	2	1	?	1	1	1	1	0	0	0	3	2	0	0	1	2	3	1
<i>Allantoxena</i>	0	5	2	1	?	1	1	1	1	0	0	0	3	2	0	0	1	2	3	1
<i>Severonis</i>	1	0	0	1	?	0	1	1	1	0	0	1	3	2	0	0	1	2	3	0
<i>Phalacrocleptes</i>	0	5	2	1	?	1	1	1	1	0	2	5	1	2	0	0	1	2	3	0
<i>Metacineta</i>	1	1	1	1	0	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Urnula</i>	1	1	1	1	0	1	0	1	1	0	0	2	3	2	0	2	1	2	3	0
<i>Paracineta</i>	1	0	0	1	0	0	1	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Actynocyathula</i>	1	1	0	1	?	0	1	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Limnoricus</i>	1	0	0	1	?	0	1	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Distarcon</i>	1	0	0	1	?	0	1	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Nipponarcon</i>	1	0	0	1	?	0	1	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Luxophrya</i>	1	0	1	1	?	0	1	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Loricophrya</i>	1	0	0	1	0	0	1	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Praethecacineta</i>	1	0	1	1	?	1	0	1	1	0	0	0	0	2	3	0	1	2	3	0
<i>Mistarcon</i>	1	1	1	1	?	1	0	1	1	0	2	5	2	2	0	2	1	2	3	0
<i>Pseudogemmides</i>	1	1	1	1	?	1	0	1	1	0	2	5	2	2	0	2	1	2	3	0
<i>Manuelophrya</i>	1	1	1	1	?	1	0	1	1	0	2	5	2	2	0	2	1	2	3	0
<i>Tachyblaston</i>	1	0	1	0	?	1	0	1	0	1	6	5	3	2	0	3	1	2	3	0
<i>Ephelota</i>	1	0	0	1	1	1	0	1	1	0	0	0	3	2	1	0	1	2	3	0
<i>Tunicophrya</i>	1	0	0	1	1	1	0	1	1	0	0	0	3	2	1	0	1	2	3	0
<i>Metephelota</i>	1	0	0	1	1	1	0	1	1	0	0	0	3	2	1	0	1	2	3	0
<i>Podocyathus</i>	1	0	0	1	1	1	0	1	1	0	0	0	3	2	1	0	1	2	3	0
<i>Shellephelota</i>	1	0	0	1	1	1	0	1	1	0	0	0	3	2	1	0	1	2	3	0
<i>Thaumatophrya</i>	1	0	0	1	1	1	0	1	1	0	0	0	3	2	1	2	1	2	3	0
<i>Ophryocephalus</i>	1	0	0	1	1	1	0	1	1	0	0	2	3	2	0	2	1	2	3	0
<i>Ophiurephelota</i>	1	0	0	1	1	1	0	1	1	0	0	1	3	2	0	0	1	2	3	0

As for macronucleus branches, their original function was probably mechanical (supporting prehensile tentacles) but this was the basis for a transition to polygemmic budding. As a result, the reproductive potential of the group considerably increased.

During adaptation to inhabiting various substrates in several ephelotins the stalk (in *Tunicophrya* Jankowski, 1973) and prehensile tentacles (in *Ophryocephalus* and *Ophiurephelota*) were lost. The oligomerization of the sucking tentacles is characteristic of parasitic forms (*Thaumatophrya*, *Ophryocephalus*). In some genera special supporting structures such as apical stalk widening (in *Podocyathus* Kent, 1881) or lorica (in *Shellephelota*) were formed.

The tendency in suctorian evolution represented by cladogram is the secondary transition to the planktonic mode of life. The reduction of the adhesive organelles in *Sphaerophrya* is associated with this tendency.

The allantosomid suctorians might be derived from planktonic podophryids. In our view, morphological relations of the genus *Vanhovenia* to sphaerophryans attest this. This genus may be considered as intermediate between two groups.

Within the second cluster the tendency to protection of stalk-zooid junction by means of formation of a regular lorica or stylothea is clearly expressed.

The tendency to submergence of the protomit into parental cell (semi-circumvagative budding) is associated with the limitation of space within lorica and manifests itself in *Paracineta* and *Metacineta*.

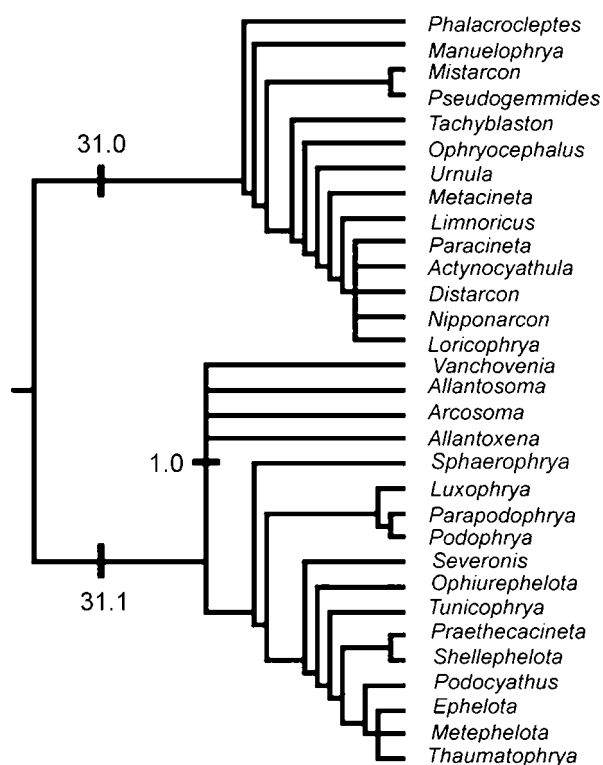
There are few substrate-specific forms among exogemmins with stylothea. *Metacineta rossica* (Jankowski, 1981) is specific to isopode crustaceans (*Asellus* Geoffroy, 1762). The tendency to host specificity is manifest in parasitic forms only.

Consequently, morphological adaptations in form of oligomerization of the tentacles (*Urnula*) and of amplification of their epiplasm (*Pseudogemmides*, *Mistarcon*, *Manuelophrya*) in genera which transitioned from commensalism to parasitism may occur.

The systematic position of the genus *Tachyblaston* was little discussed. In the scheme of phylogenetical relations obtained (Fig. 14) *Tachyblaston* falls into a common group with loricate genera. Aside from the presence of stylothea in a state of dactylozoit, the semi-circumvagative budding with

Table 2. (Continuation)

Taxa	Characters															
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Didinium</i> (outgroup)	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Parapodophrya</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Podophrya</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Sphaerophrya</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Vanchovenia</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Allantosoma</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Arcosoma</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Allantoxena</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Severonis</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Phalacrocleptes</i>	3	2	3	3	2	0	1	3	4	2	1	3	4	4	1	0
<i>Metacineta</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	1	1	0
<i>Urnula</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	1	1	0
<i>Paracineta</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Actynocyathula</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Limnoricus</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	2	1	0
<i>Distarcon</i>	2	2	3	3	2	1	1	3	4	2	0	1	2	0	1	0
<i>Nipponarcon</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Luxophrya</i>	1	2	1	0	2	1	1	3	4	2	1	3	4	3	0	0
<i>Loricophrya</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Praethecacineta</i>	1	2	1	3	2	1	0	0	0	0	1	3	4	3	1	0
<i>Mistarcon</i>	3	2	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Pseudogemmides</i>	3	2	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Manuelophrya</i>	3	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Tachyblaston</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Ephelota</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	2
<i>Tunicophrya</i>	0	0	3	3	2	0	1	3	4	2	1	3	4	3	1	2
<i>Metephelota</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	2
<i>Podocyathus</i>	1	2	1	1	2	0	1	3	4	2	1	3	4	3	1	2
<i>Shellephelota</i>	1	2	1	1	2	1	0	0	0	0	1	3	4	3	1	2
<i>Thaumatophrya</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	2
<i>Ophryocephalus</i>	1	2	1	3	2	0	1	3	6	2	2	0	1	1	1	2
<i>Ophiurephelota</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	1



lateral position of the protomit brings these genera closer together.

In our opinion, the position of *Tachyblaston* in the cladogram reflects its actual affinity with metacinetins and paracinetins.

### Phylogenetic relations within vermigemmins

The morphological characters and features of reproduction of 22 genera were analyzed (Table 3). As a result we obtained about 100 equal trees with length 91, ci=75 and ri=85.

The consensus cladogram (Fig. 15) contains two major groups which include genera with capitate tentacles (11.0) and both rod-like (11.2) and ramified (11.5 – genus *Shyzactinia*) tentacles.

Two groups of genera the representatives of which possess actinophores (17.0) (*Dendrosomides*, *Asterifer*,

◀ Fig. 14. Phylogenetical relationships of the genera within exogemmin suctorians. The numbers of principal apomorphies correspond to those in the list of characters.

etc.) or, alternatively, lack special carrying tentacle structures (17.1) can be outlined within vermigemmin cluster characterized by capitate tentacles.

Unloricate dentacinet suctorians with flexible tentacles fall into the same group as loricate thecacinetids due to the absence of actinophores. The position of the genera *Cucumophrya* Kunz, 1938 and *Spelaeophrya* Stammer, 1935 is due to the same reasons. It is unlikely that similarity as to this character is a consequence of affinity between the genera. This combination is probably a result of parallelism.

The genera *Hastarcon*, *Trophogemma*, *Spinarcon* and *Vostonica* with actinophores of different shape (18.1) give rise to a distinct group within the cluster characterized by presence of rod-like (11.2) or ramified (11.5) tentacles. The second group combines the genera with «proboscis-like» (trunk) actinophores (19.2). The genus *Shyzactinia* with ramified tentacles (11.5) is an exception. However, the genus indubitably has affinity with other “trunk-bearing” genera.

Nevertheless, the cladogram gives a reasonable fit to phylogenetical relations of vermigemmin suctorians.

Contrary to exogemmins, in which specificity to host or substrate is not very common, the vermigemmins (excluding genera *Spongiarcon*, *Spelaeophrya*, *Leboransia*, *Trophogemma* and a few representatives of *Ophryodendron* and *Thecacineta*) inhabit exclusively harpacticoid crustaceans. It seems plausible that the group owes its origin to the transition to commensalism on harpacticoids. As it was discussed above, the

vermigemmic budding is an adaptation to hydrodynamic conditions near the body surface of the crustacean hosts (mainly harpacticoids).

Vermigemmins are one of the few suctorian groups whose phylogeny has been discussed. A.V. Jankowski’s (1994) hypothesis is that *Rhabdophrya* is the most primitive genus of vermigemmin suctorians. From this morphotype the genera *Dendrosomides*, *Rondosomides*, *Trophogemma*, *Crevicometes*, *Hastarcon*, etc. are derived. However, this phylogenetic lineage was discussed without considering the type of the tentacle.

In our view, vermigemmin suctorians might be derived from exogemmins. Two evolutionary lineages (with conservation of capitate tentacles and with formation of rod-like tentacles) were generated shortly after transition of the ancestral group to inhabiting harpacticoids.

The forms with clavate tentacles related to the genera *Lecanophrya* or *Spelaeophrya* are probably the most primitive vermigemmins. The subsequent divergence of the group was associated mostly with amplification of function of the prey capture that results in ramification of body, the shape of actinophores and the formation of flexible agile tentacles.

The genus *Rhabdophrya* is probably closest to the initial group of the second lineage from which the genera *Spinarcon*, *Trophogemma*, *Hastarcon*, *Vostonica* and *Ophryodendron* can be derived. This idea is to some extent consistent with A.V. Jankowski’s (1994) view.

**Table 3.** States of the generic characters within Vermigenia (explanation are in the list of characters).

Taxa	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Didinium</i> (outgroup)	0	5	2	1	0	1	1	1	1	1	6	5	3	2	0	3	1	2	3	1
<i>Spelaeophrya</i>	1	2	1	1	?	1	1	0	1	0	0	0	3	2	0	0	1	2	3	0
<i>Lecanophrya</i>	1	2	1	1	?	1	1	0	1	0	0	1	3	2	0	0	0	0	0	0
<i>Lecanophryella</i>	1	2	1	1	?	1	1	0	1	0	0	1	3	2	0	0	0	1	0	0
<i>Dendrosomides</i>	1	2	1	1	?	1	1	0	1	0	0	0	3	2	0	0	0	1	0	0
<i>Rondosomides</i>	1	2	1	1	?	1	1	0	1	0	0	0	3	2	0	0	0	1	0	0
<i>Cucumophrya</i>	1	2	1	1	?	1	1	0	1	0	0	0	3	2	0	0	1	2	3	0
<i>Asterifer</i>	1	2	1	1	?	1	1	0	1	0	0	0	3	2	0	0	0	1	0	0
<i>Leboransia</i>	1	2	1	1	?	1	1	0	1	0	0	0	3	2	0	0	0	0	0	0
<i>Dentacineta</i>	1	2	1	1	?	1	1	0	1	0	0	2	3	2	0	0	1	2	3	0
<i>Pleurophryodendron</i>	1	2	1	1	?	1	1	0	1	?	?	?	?	?	?	?	?	?	?	0
<i>Thecacineta</i>	1	2	1	1	0	1	1	0	1	0	0	0	3	2	0	0	1	2	3	0
<i>Ophryodendron</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	0	1	2	0
<i>Corethrya</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	0	1	2	0
<i>Shyzactinia</i>	1	2	1	1	?	1	1	0	1	0	5	5	3	0	0	0	0	1	2	0
<i>Spongiarcon</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	0	1	2	0
<i>Loricodendron</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	0	1	2	0
<i>Rhabdophrya</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	1	2	3	0
<i>Crevicometes</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	0	1	2	0
<i>Hastarcon</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	0	1	0	0
<i>Spinarcon</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	1	2	3	0
<i>Trophogemma</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	0	1	0	0
<i>Vostonica</i>	1	2	1	1	?	1	1	0	1	0	2	5	0	2	0	0	0	1	0	0

Table 3. (Continuation)

Taxa	Characters															
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Didinium</i> (outgroup)	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Spelaeophrya</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Lecanophrya</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	0
<i>Lecanophryella</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	0
<i>Dendrosomides</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	2
<i>Rodosomides</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Cucumophrya</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Asterifer</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Leboransia</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Dentacineta</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Pleurophryodendron</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Thecacineta</i>	1	2	1	3	2	1	0	0	0	0	1	3	4	3	1	0
<i>Ophryodendron</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	1
<i>Corethrya</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	1
<i>Shyzactinia</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	1
<i>Spongiarcon</i>	1	2	2	3	2	0	1	3	4	2	1	3	4	3	1	1
<i>Loricodendron</i>	0	0	3	3	2	1	1	3	4	2	0	0	0	0	1	1
<i>Rhabdophrya</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Crevicometes</i>	0	0	3	3	2	0	1	3	4	2	1	3	4	3	1	1
<i>Hastarcon</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Spinarcon</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	1
<i>Trophogemma</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	1
<i>Vostonica</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0

The origin of ramified tentacles in *Shyzactinia* was associated with ophryodendrids development.

One further comment should be made. Vermigemmin suctorians are specialized mainly to one taxa of the host (harpacticoid copepods). Thus, their

divergence is relatively less than in exogemmins or especially in endogemmins that will be discussed below. This divergence level also accounts for high values of consistency index (75) and retention index (85).

### Phylogenetic relations within endogemmins

A discussible cladogram for endogemmin genera was difficult to obtain due to abundance of genera (51) and the high incidence of homoplasy. Therefore, the stalked (25 genera) and unstalked (26 genera) endogemmins, usually separated by investigators (Janowski, 1981; Batisse, 1994), were analysed separately (Tables 4 and 5).

The consensus cladogram (Fig. 16), based on 100 parsimonomic trees (length 89, ci=65, ri=83), represents the phylogenetic relations between genera of stalked endogemmin suctorians.

The first group includes several genera distinguished by only one or two characters, mostly associated with tentacle morphology (*Choanophrya* by funnel-like tentacles (11.4), *Dactylostoma* by finger-like ones (12.4), *Andrusovia* and *Talizona* by flexible ones (12.2), etc.). It is our opinion that similar specializations of capitate tentacle to different food in the genera listed above were derived

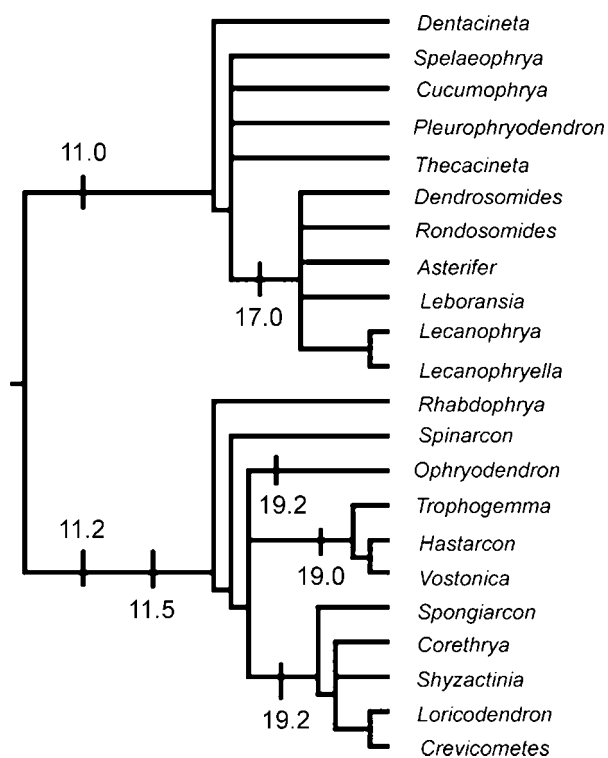


Fig. 15. Phylogenetic relationships of the genera within vermigemmin suctorians. The numbers of principal apomorphies correspond to those in the list of characters.



independently. Thus, the similarity between the genera in this case does not point to affinity between them.

The genera with mucous lorica (35.0) are included into the second group (*Rondacineta* Jankowski, 1978, *Cryptacineta* Jankowski, 1978 and *Cryptophrya* Jankowski, 1973). However, it is unlikely that the presence of the mucous lorica may be thought of as a synapomorphic character.

Another group of related genera (by such synapomorphic character as lack of the lorica – 26.0) is characterized by different stalk morphology and the presence of various actinophores.

The position of *Parastylophrya* Jankowski, 1978 has attracted our attention because the genus was previously considered as related to unstalked trichophryins (under the name *Digitophrya* Matthes, 1988<sup>4</sup>). It turned out that *Parastylophrya* is actually closer to a tokophryin genus *Listarcon* Jankowski, 1982 but differs from it by the presence of ramified macronucleus (36.2) and actinophores (17.0).

The genera with regular tectinous lorica (27.0) or stylotheca (31.0) form the third large group.

The group includes 26 genera of unstalked endogemins (Fig. 17) partitioned into two clusters and seven

lower-order groups with different combinations of synapomorphies at the consensus tree (length 99, ci=55, ri=80) that is in turn based upon 100 equal trees.

The genera of intracellular parasites of ciliates and molluscs (*Parendosphaera* and *Endosphaera*) and parasites of turbellarian parenchyma (*Acoelophthirius* Jankowski, 1981) are in the first cluster. Complete reduction of tentacles (10.1), and the presence of a characteristic swarmer with perforatorium (9.0) unite these genera.

These genera fall near the outgroup due to lack of tentacles and adhesive organelles.

The genera with tentacles (10.0) are united into the second cluster.

Within this cluster there falls the group of genera whose representatives lead planktonic mode of life – *Mucophrya*, *Tetraedrophrya*, *Marinecta*, *Astrophrya*, *Staurophrya*). The latter two genera are united by the presence of actinophores (17.0).

The genera characterized by the stylotheca (31.0) are included into another group. Ectoparasitic suctorians with rod-like tentacle (11.2) also performing the function of adhesion (*Pottsiocles*, *Pseudogemma*) belong to this group. The planktonic genus *Sphaeracineteta* Jankowski, 1987 and the sessile genus with capitate tentacles *Solenophrya* Claparede et Lachmann, 1859 are also in this group, yet parallelisms can not be ruled out.

<sup>4</sup> *Digitophrya* is both synonymous and homonymic name (see Corliss, 1979, p. 208 and Aescht, 2001, p. 59).

**Table 4.** States of the generic characters within stalked Endogenia (explanation are in the list of characters).

Taxa	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Didinium</i> (outgroup)	0	5	2	1	0	1	1	1	1	1	6	5	3	2	0	3	1	2	3	1
<i>Acinetides</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	0	0	0	0
<i>Acineta</i>	1	3	2	1	0	1	0	1	1	0	0	0	3	2	0	0	0	0	0	0
<i>Trematosoma</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	0	0	0	0
<i>Soracineta</i>	1	3	2	1	?	1	0	1	1	0	0	2	3	2	0	1	0	0	0	0
<i>Anthacineta</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	0	0	0	0
<i>Cryptacineta</i>	?	?	?	?	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Phyllacineta</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Cryptophrya</i>	?	?	?	?	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Rondacineta</i>	?	?	?	?	?	1	0	1	1	0	0	1	3	2	0	0	1	2	3	0
<i>Slitarcon</i>	1	3	2	1	0	1	0	1	1	?	?	?	?	?	0	?	1	2	3	0
<i>Vasacineta</i>	1	3	2	1	0	1	0	1	1	0	0	2	3	2	0	0	1	2	3	0
<i>Acinetopsis</i>	1	3	2	1	0	1	0	1	1	0	0	3	3	2	0	0	1	2	3	0
<i>Veracineta</i>	1	3	2	1	0	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Tokophrya</i>	1	3	2	1	0	1	0	1	1	0	0	0	3	2	0	0	0	0	0	0
<i>Tokophryopsis</i>	1	3	2	1	0	1	0	1	1	0	0	0	3	2	0	0	0	0	0	0
<i>Lecanodiscus</i>	1	?	?	?	?	?	?	?	?	?	0	0	0	3	2	0	0	1	2	3
<i>Listarcon</i>	1	?	?	?	?	?	?	?	?	?	0	0	0	3	2	0	0	1	2	3
<i>Pelagacineta</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Corynophrya</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Andrusovia</i>	?	?	?	?	?	?	?	?	?	?	0	0	2	3	2	0	0	1	2	3
<i>Dactylostoma</i>	?	?	?	?	?	?	?	?	?	?	0	0	4	3	2	0	0	1	2	3
<i>Talizona</i>	1	?	?	?	?	?	?	?	?	?	0	0	2	3	2	0	1	1	2	3
<i>Parastylophrya</i>	?	?	?	?	?	?	?	?	?	?	0	0	0	3	2	0	0	0	1	0
<i>Squalorphrya</i>	?	?	?	?	?	?	?	?	?	?	0	0	0	3	2	0	0	1	2	3
<i>Choanophrya</i>	1	3	2	1	?	1	0	1	1	0	4	5	3	2	0	0	1	2	3	0

**Table 4.** (Continuation)

Taxa	Characters															
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Didinium</i> (outgroup)	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Acinetides</i>	1	2	3	3	2	1	1	3	4	2	0	0	0	2	1	0
<i>Acineta</i>	1	2	1	0	2	1	0	0	0	1	1	3	4	3	1	0
<i>Trematosoma</i>	1	2	1	0	2	1	0	0	0	1	1	3	4	3	1	0
<i>Soracineta</i>	1	2	1	0	2	1	0	0	0	1	1	3	4	3	1	0
<i>Anthacineta</i>	1	2	1	3	2	1	0	1	0	2	1	3	4	3	1	0
<i>Cryptacineta</i>	1	2	1	0	2	1	1	3	4	2	1	3	4	3	0	0
<i>Phyllacineta</i>	1	2	1	3	2	1	0	0	0	1	1	3	4	3	1	0
<i>Cryptophrya</i>	1	2	1	0	2	1	1	3	4	2	1	3	4	3	0	0
<i>Rondacineta</i>	1	2	1	0	2	1	1	3	4	2	1	3	4	3	0	0
<i>Slitarcon</i>	1	2	1	3	2	1	0	0	0	1	1	3	4	3	1	0
<i>Vasacineta</i>	1	2	1	3	2	1	0	0	0	0	1	3	4	3	1	0
<i>Acinetopsis</i>	1	2	1	3	2	1	0	0	0	1	1	3	4	3	1	0
<i>Veracineta</i>	1	2	1	3	2	1	0	0	0	1	1	3	4	3	1	0
<i>Tokophrya</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	0
<i>Tokophryopsis</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	0
<i>Lecanodiscus</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	0
<i>Listarcon</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Pelagacineta</i>	1	2	1	1	2	0	1	3	4	2	1	3	4	3	1	2
<i>Corynophrya</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	1
<i>Andrusovia</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	0
<i>Dactylostoma</i>	1	2	1	1	2	0	1	3	4	2	1	3	4	3	1	0
<i>Talizona</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	0
<i>Parastylophrya</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	2
<i>Squalorophrya</i>	1	2	1	3	2	1	1	3	4	2	1	3	4	3	0	1
<i>Choanophrya</i>	1	2	1	2	2	0	1	3	4	2	1	3	4	3	1	0

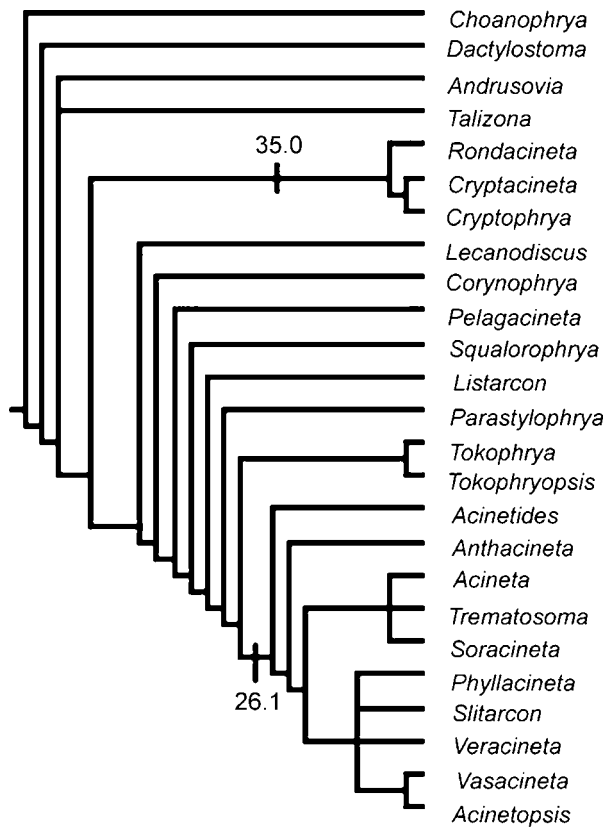
The genera attaching to the substrate by the body surface or protuberances (31.1), by the cinctum (21.4) or by specialized tentacles (as *Capriniana* – 21.3) are pooled into a large group.

**Table 5.** States of the generic characters within stalkless Endogenia (explanation are in the list of characters).

Taxa	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Didinium</i> (outgroup)	0	5	2	1	0	1	1	1	1	1	6	5	3	2	0	3	1	2	3	1
<i>Rhizobranhium</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Peltacineta</i>	1	3	2	1	?	1	0	1	1	0	2	5	0	2	0	0	1	2	3	0
<i>Anarma</i>	?	?	?	?	?	?	?	?	?	0	0	0	3	2	0	0	1	2	3	0
<i>Muscophrya</i>	?	?	?	?	?	?	?	?	?	0	0	1	3	2	0	0	1	2	3	0
<i>Trichophrya</i>	1	3	2	1	1	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Brachyosoma</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Dendrosoma</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	0	1	1	0
<i>Riftius</i>	1	3	2	1	?	1	0	1	1	0	0	2	3	2	0	0	1	2	3	0
<i>Gorgonosoma</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	0	1	1	0
<i>Mucophrya</i>	?	?	?	?	?	?	?	?	?	0	0	0	3	2	0	0	1	2	3	1
<i>Stylophrya</i>	1	3	2	1	1	1	0	1	1	0	0	0	3	2	0	0	0	1	0	0
<i>Chenophrya</i>	1	3	2	1	1	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Solenophrya</i>	?	?	?	?	?	?	?	?	?	0	0	0	3	2	0	0	1	2	3	0
<i>Astrophrya</i>	?	?	?	?	?	?	?	?	?	0	0	0	3	2	0	0	0	1	0	1
<i>Erastophrya</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	0
<i>Tetraedrophrya</i>	?	?	?	?	?	?	?	?	?	0	0	0	3	2	0	0	1	2	3	1
<i>Parendosphaera</i>	1	3	2	1	?	1	1	1	0	1	6	5	3	2	0	3	1	2	3	1
<i>Marinecta</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	1
<i>Pseudogemma</i>	1	3	2	1	1	1	0	1	1	0	2	5	2	2	0	2	1	2	3	0
<i>Rhyncheta</i>	1	3	2	1	?	1	0	1	1	0	0	2	3	2	0	2	1	2	3	0
<i>Acoelophthyrus</i>	1	3	2	1	?	1	1	1	0	1	6	5	3	2	0	3	1	2	3	1
<i>Capriniana</i>	1	3	2	1	?	1	0	1	1	0	0	0	2	2	0	0	1	2	3	0
<i>Staurophrya</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	0	0	1	
<i>Sphaeracineta</i>	1	3	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	1
<i>Pottsiocles</i>	1	3	2	1	?	1	1	1	0	0	2	5	2	2	0	0	1	2	3	0
<i>Endosphaera</i>	1	3	2	1	?	1	1	1	0	1	6	5	3	2	0	3	1	2	3	1

Table 5. (Continuation)

Taxa	Characters															
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Didinium</i> (outgroup)	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Rhizobranchiun</i>	0	0	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Peltacineta</i>	0	0	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Anarma</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	1
<i>Muscophrya</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Trichophrya</i>	0	0	3	3	2	0	1	3	4	2	1	3	4	3	1	2
<i>Brachyosoma</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Dendrosoma</i>	0	0	3	3	2	0	1	3	4	2	1	3	4	3	1	2
<i>Riftus</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Gorgonosoma</i>	0	0	3	3	2	0	1	3	4	2	1	3	4	3	1	2
<i>Mucophrya</i>	5	2	3	3	2	1	1	3	4	2	1	3	4	3	0	0
<i>Stylophrya</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Chenophrya</i>	4	2	3	3	1	0	1	3	4	2	1	3	4	3	1	1
<i>Solenophrya</i>	0	0	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Astrophrya</i>	5	2	3	3	2	1	1	3	4	2	1	3	4	3	0	?
<i>Erastophrya</i>	4	2	3	3	0	0	1	3	4	2	1	3	4	3	1	0
<i>Tetraedrophrya</i>	5	2	3	3	2	1	1	3	4	2	1	3	4	3	0	?
<i>Parendosphaera</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Marinecta</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	1
<i>Pseudogemma</i>	3	2	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Rhyncheta</i>	0	0	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Acoelophthyrius</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Capriniana</i>	3	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Staurophrya</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Sphaeracineta</i>	5	2	3	3	2	1	1	3	4	2	0	0	0	3	1	0
<i>Pottsiocles</i>	3	2	3	3	2	1	1	3	4	2	0	0	0	0	1	0
<i>Endosphaera</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0



Finally, a compact group is formed by the genera whose representatives bear well-developed actinophores (17.0).

It should be mentioned that, as with all other cladograms, there are many cases of homoplasy in the scheme obtained (ci=55). Nevertheless, the cladogram adequately represented the affinities between taxa.

Since the internal budding derives from semi-circumvaginate one, it is reasonable to suggest that their ancestors were exogemmins with the same mode of reproduction. However, it is unlikely that these were any metacinetids. In our opinion, the ancestors of endogemmins were most likely related to podophryins.

Some tokophryans have almost spherical body, tentacles that are not arranged in fascicles and podophrya-like stages of metamorphosis. These suctorians are probably the ones most close to the parental group.

The ancestors of endogemmins were probably not specialized to inhabiting particular substrates or hosts. At the same time, advanced protection of protomits was favourable for high ecological plasticity of the group.

◀ Fig. 16. Phylogenetical relationships of the genera within stalked endogemmin suctorians. The numbers of principal apomorphies correspond to those in the list of characters.

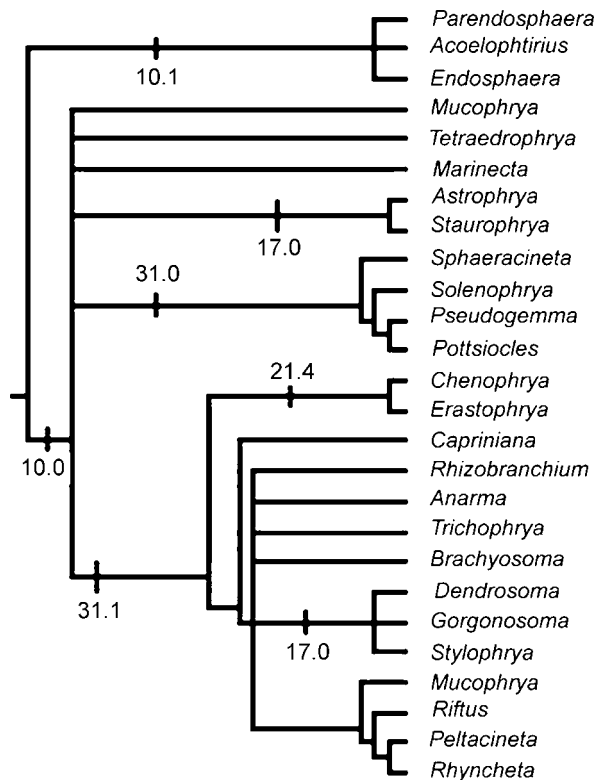


Fig. 17. Phylogenetical relationships of the genera within stalkless endogemmin suctorians. The numbers of principal apomorphies correspond to those in the list of characters.

The endogemmins occupied a wide range of substrates and hosts that caused intensive speciation in the group. As a result, about a half of suctorian genera and species fall into Endogenia Collin, 1912. All morphotypes characteristic of suctorians are represented among endogemmins. All the modes of attachment organelles and all three types of lorica are present in them. The diversity of tentacle morphology is lower than in other groups, but quite advanced differentiation of the tentacles into hunting and sucking ones also took place (*Acinetopsis*). Thus, all evolutionary tendencies discussed in chapter 2 were manifest in development of endogemmin suctorians.

### Phylogenetic relations within evaginogemmins

Morphological characters and features of reproduction in 20 genera were analyzed (Table 6). As a result we obtained more than 100 trees with length 94,  $ci=74$  and  $ri=85$ .

It may be inferred from the consensus cladogram that suctorians with inversogemmy fall into four groups (Fig. 18).

The first cluster includes genera (*Tripanococcus*, *Cyathodinium*, *Enchelyomorpha*, *Stylocometes* and *Discosomatella*) distinguished only by one or two apomorphic characters.

The position of *Cyathodinium* should be discussed. The representatives of the genus from intestine of guinea pigs have a unique type of tentacles (endosprits (11.3)) and ciliary trophont. The genus was previously classified as a taxon of high rank (subclass Neotenea Jankowski, 1978) or transferred into the family Discophryidae (Batisse, 1994). However, in this instance, the genus is situated near with the genera with rod-like tentacles or reduced ones (*Tripanococcus*).

Parasites of rotifers tissue from the genus *Tripanococcus* are recognized as relatives of discophryins (Batisse, 1994) but positioned near dendrocometids.

In our opinion, the position of both *Tripanococcus* and *Cyathodinium* in the scheme (Fig. 18) is associated with several plesiomorphic characters, like the absence of tentacles. However, in our view it is unreasonable to consider the forms specialized to parasitism or commensalism in mammal intestine as relatives of possible ancestors of inversogemmin suctorians.

The genera with rod-like (11.2) or ramified (11.5) tentacles fall in two other clusters. First of all, the unusual position of the genus *Stylocometes* attracted our attention. A.V. Jankowski (1981) placed *Stylocometes*, discophryins and the genera *Echinophrya*, *Enchelyomorpha* and *Discosomatella* near the group of genera bearing branched tentacles. At the same time, the genera with ramified tentacles form a compact group.

The genera with clavate tentacles are combined in another large cluster. The genera with a disc-like spread body (*Heliophrya* and *Cyclophrya*), disc-like stalked body (*Discophrya*, *Setodiscophrya*, *Misacineta* and *Elatodiscophrya*) and three loricate suctorian genera (*Periacineta*, *Kormosia* and *Peridiscophrya*) form compact groups within the cluster.

The position of the unloricate genus *Prodiscophrya* Kormos, 1935 within the latter group can be attributed to similarity of the conjugation mode with that in the genus *Kormosia*. In turn, for genus *Prodiscophrya* a variety of plesiomorphic characters (arrangement of the tentacles round the body, spherical cell) is characteristic. In spite of the characters listed, *Parapodophrya* is probably the most primitive genus of inversogemmins closely allied to the ancestral form of the group.

All inversogemmin suctorians living in fresh waters and freshwater exogemmins related to *Podophrya* or *Parapodophrya* may be thought as most probable ancestors of the group. The morphological characteristics of representatives of *Prodiscophrya* from freshwater periphyton partially testify in favour this view.

**Table 6.** States of the generic characters within Evaginogenia (explanation are in the list of characters).

Taxa	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Didinium</i> (outgroup)	0	5	2	1	0	1	1	1	1	1	6	5	3	2	0	3	1	2	3	1
<i>Prodiscophrya</i>	1	4	2	1	2	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Discophrya</i>	1	4	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Setodiscophrya</i>	1	4	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Misacineta</i>	1	4	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Periacineta</i>	1	4	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Kormosia</i>	1	4	2	1	2	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Elatodiscophrya</i>	1	4	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Peridiscophrya</i>	1	4	2	1	?	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Rhynchophrya</i>	1	4	2	1	?	1	0	1	1	0	0	2	3	2	0	0	1	2	3	2
<i>Heliophrya</i>	1	4	2	1	0	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Cyclophrya</i>	1	4	2	1	0	1	0	1	1	0	0	0	3	2	0	0	1	2	3	2
<i>Tripanococcus</i>	1	4	2	1	?	1	0	1	0	1	6	5	3	2	0	3	1	2	3	2
<i>Stylocometes</i>	1	4	2	1	0	1	0	1	1	0	2	5	0	2	0	0	1	2	3	2
<i>Dendrocometes</i>	1	4	2	1	?	1	0	1	1	0	5	5	3	0	0	0	1	2	3	2
<i>Echinophrya</i>	1	?	?	?	?	?	?	?	?	0	2	5	0	2	0	0	1	2	3	2
<i>Discosomatella</i>	1	?	?	?	?	?	?	?	?	0	2	5	0	2	0	0	1	2	3	2
<i>Niscometes</i>	1	4	2	1	?	1	0	1	1	0	5	5	3	1	0	0	1	2	3	2
<i>Cometodendron</i>	1	?	?	?	?	?	?	?	?	0	5	5	3	0	0	0	1	1	0	0
<i>Cyathodinium</i>	1	4	2	1	?	1	0	1	1	0	3	5	3	2	0	0	1	2	3	2
<i>Encheliomorpha</i>	1	4	1	1	?	0	1	1	1	0	2	5	0	2	0	0	1	2	3	2

The development of this suctorian group was probably associated with transition to inhabiting freshwater invertebrates.

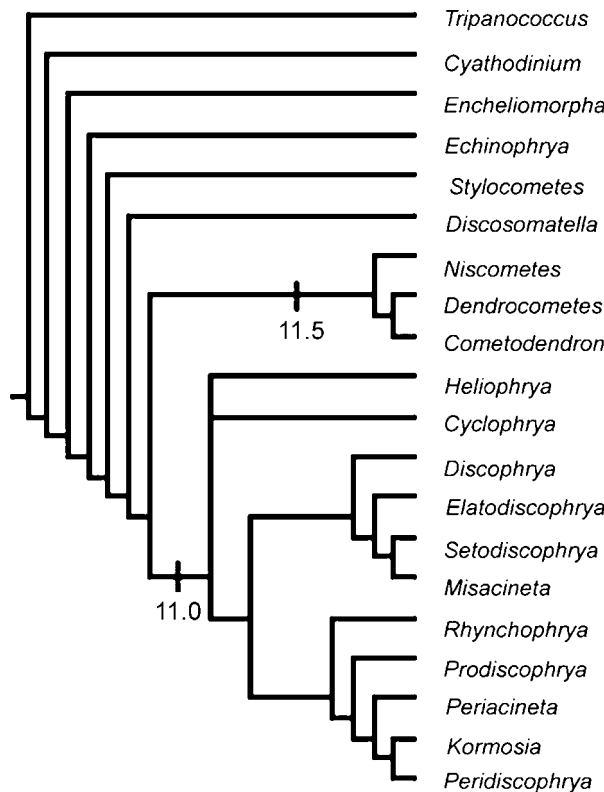
In part, the phylogeny of the forms that retained capitate tentacles is probably associated with the colonization of water beetles and bugs. Similar to adults of harpacticoid copepods for vermigemmins, a long-

living (not moulting) imago of insects turned out to be a convenient substrate for inversogemmins. Notably, these suctorians do not occur on larval stages of insects.

Some inversogemmins live in periphyton. Topical competition with diatoms is an important factor in peryphyton conditions (Dovgal, 1994). The suctorians can avoid the competition colonizing the substrates in streams with critical velocity for diatoms (Dovgal and Kochin, 1995). The formation of spread body is one of the most widespread adaptations among suctorians. We associate the origin of heliophryids with this adaptation.

As for the genus *Encheliomorpha*, it is probably an example of early transition to the planktonic mode of life in anaerobic conditions. Consequently, the representative of the genus retained an ancestral character (spherical body) but formed the rod-like tentacles and a swarmer similar to *Parapodophrya* in parallel.

Judging from some primitive characters of dendrocometin budding (Batisse, 1975), these suctorians probably diverged early from other inversogemmins under transition to inhabiting crustaceans. The tendency to formation of rod-like tentacles is characteristic for the group that presumably lived under conditions of good aeration in oligotrophic water bodies. Subsequent amplification of the tentacle function at the expense of formation of ramified



◀ Fig. 18. Phylogenetical relationships of the genera within evaginogemmin suctorians. The numbers of principal apomorphies correspond to those in the list of characters.

Table 6. (Continuation)

Taxa	Characters															
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Didinium</i> (outgroup)	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Prodiscophrya</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Discophrya</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	0
<i>Setodiscophrya</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	2
<i>Misacineta</i>	1	2	1	0	2	0	1	3	4	2	1	3	4	3	1	1
<i>Periacineta</i>	1	2	1	3	2	1	0	0	0	1	1	3	4	3	1	0
<i>Kormosia</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	2	1	0
<i>Elatodiscophrya</i>	1	2	1	1	2	0	1	3	4	2	1	3	4	3	1	1
<i>Peridiscophrya</i>	2	2	3	3	2	1	1	3	4	2	0	0	0	0	1	1
<i>Rhynchophrya</i>	1	2	1	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Heliophrya</i>	0	0	0	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Cyclophrya</i>	0	0	0	3	2	0	1	3	4	2	1	3	4	3	1	2
<i>Tripanococcus</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Stylocometes</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Dendrocometes</i>	0	0	0	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Echinophrya</i>	1	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Discosomatella</i>	0	0	0	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Niscometes</i>	0	0	0	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Cometodendron</i>	0	1	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Cyathodinium</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0
<i>Encheliomorpha</i>	5	2	3	3	2	0	1	3	4	2	1	3	4	3	1	0

tentacles and even branching of the body (in *Cometodendron* Swarczewsky, 1928) was associated with life under conditions of insufficient food resources.

The origin of the *Cyathodinium* and *Tripanococcus* is yet to be explained. It is possible that in the former, as A.V. Jankowski (1981) and A. Batisse (1994) pointed

out, neoteny took place. The reduction of feeding organelles and features of budding (sequential poly-inversogemmy) in the latter case are unquestionably the results of specialization to parasitism. However, at present possible ancestors of these groups can not be named.

## CHAPTER 5. PRINCIPLES OF TAXONOMY AND NEW CLASSIFICATION OF SUCTOREA

As indicated above, similar evolutionary tendencies are manifest in taxa that differ by the mode of budding but probably with different sequences. Thus, relative taxonomical values of the characters are variable in different lineages. For example, vermigemmins are distinguished by the type of tentacles and morphology of actinophores (Fig. 15). In contrast, in exogemmins the branches of the first order are determined by the morphology of adhesive structures and those of the second order, by the type of the tentacles (Fig. 14). In the course of systematic revision we took this into account alongside with our view on the evolution of different structures and the results of cladistic analysis.

As the phylogenetic implications of Chapter 4 suggest, three different levels of affinity can be distinguished in Suctorea. In our opinion the levels are consistent with taxonomical ranks, the highest rank being determined by the type of budding. Other ranks are determined by the combinations of the tentacle type, presence (or absence) of lorica, mode of actinophores, modes of attachment to substrate, etc.

As a result, we conserve the subdivision of the class Suctorea into subordinate taxa by the mode of budding as proposed by A.V. Jankowski (1978, 1980, 1981). Consequently, we accept four subclasses: Exogenia Collin, 1912 (named Tomogenea by A.V. Jankowski), Vermigenia Jankowski, 1978, Endogenia and Evaginogenia. Considering that inversogemmy was indicated as a type of cyathodiniid reproduction (Paulin and Corliss, 1969) we classify this group in Evaginogenia and eliminate the subclass Neotenea Jankowski, 1978.

The characters like presence (or absence) of lorica, additional prehensile organelles, features of the life cycle, etc. characterize the orders in exogemmin suctorians. Consequently, we distinguish the following traditional orders within Exogenia: Podophryida Jankowski, 1967 (unloricate forms with spherical or asymmetrical body), Metacinetida Jankowski, 1978 (loricate suctorians) and Ephelotida Raabe, 1964 (suctorians with additional prehensile tentacles). The order names Paracinetida Jankowski, 1978 and Urnulida Jankowski, 1978 are synonymized with

Metacinetida Jankowski, 1978 and Allantosomatida Jankowski, 1978 with Podophryida Jankowski, 1967.

As indicated above, the monotypical genus *Tachyblaston* is usually placed near ephelotid suctorians. For the type species of the genus (*T. ephelotensis* Martin 1909, Fig. 20, J) a unique life cycle is characteristic. The trophont of *Tachyblaston* is entirely immersed into the host's (*Ephelota* sp.) cell but retains the contact with the environment (Grell, 1950, 1967). After the growth period a succession of buddings producing several ciliary swimmers occurs. After the adhesion to the substrate [hydroids (Collin, 1912) or algae (Gassovsky, 1916)] the swimmer produces a loricate "dactylophrya" stage. This stage was previously (Collin, 1909, 1912) described as a separate suctorian genus and species *Dactylophrya roscovita* Collin, 1909. It was found (Grell, 1950) that the structures of "dactylophrya" indicated as "bottle-like" tentacles are in fact the next migratory stage – dactylozoites. Dactylozoites lack ciliature and float passively until the contact with a host cell (Grell, 1967) where a new trophont forms. The organism with such a unique set of characters should undoubtedly be classified into a separate taxon of a high rank. Thus, following A.V. Jankowski, we accept the order Tachyblastonida Jankowski, 1978 with a single family Tachyblastonidae Grell, 1970.

A.V. Jankowski (1978) proposed to erect the order Phalacrocleptida (with unclear systematic position) for small oval suctorians without stalk and lorica but with numerous very short tentacles on the basal body surface. The single species *Phalacrocleptes verruciformis* (Fig. 19, I) parasitizing on polychaetes is included into the order.

*Phalacrocleptes* is an extremely specialized parasite that lacks both ciliature and infraciliature at all stages of the life cycle. The tentacles are also reduced, very short, only with an external microtubular layer and a single haptocyst (Lom and Kozloff, 1967). They probably serve for attachment only. According to E. Kozloff's (1966) observations, *P. verruciformis* reproduces by binary fission (Fig. 8, B).

In our opinion according to the combination of characters these organisms should be placed into the subclass Exogenia as the order Phalacrocleptida Jankowski, 1978 with one family Phalacrocleptidae Kozloff, 1966.

Within the order Podophryida we accept the traditional families Podophryidae Bütschli, 1889, Allantosomatidae Jankowski, 1978 and the family Severonidae Jankowski, 1981 proposed for the forms that attach to the substrate by numerous short protuberances of the body.

The families Metacinetidae Bütschli, 1889 and Paracinetidae Jankowski, 1978 are included in the order Metacinetida.

The taxonomical rank and systematic position of some taxa need further comments. In particular, it concerns the family Urnulidae Fraipont, 1878 that was proposed for ectoparasite suctorians with stylotheca and a single (or from two to three according to early authors (Claparede and Lachmann, 1861) agile tentacle. The family was not accepted by several authors. However, A.V. Jankowski (1978, p. 493) elevated their taxonomical rank up to the order with a short diagnosis: «small loricate parasitic forms with a single apical tentacle».

In fact, the representatives of the group are related to metacinetid suctorians and differ from them only by oligomerization of the tentacles and their mobility. These characters are enough to retain a separate genus *Urnula* Claparede et Lachmann, 1861 but insufficient for the erection of an order or a family. Therefore we transfer the genus *Urnula* into Metacinetidae Collin, 1912. The name Urnulidae Fraipont, 1878 is synonymized with Metacinetidae Collin, 1912.

The genus *Praethecacineteta* Matthes, 1956 had been included into the family Thecacinetidae Matthes, 1956 but was later transferred (Dovgal, 1996) into the subclass Exogenia and order Metacinetida on the basis of the mode of budding (external with laterally positioned ciliary protomit) and the type of lorica with the rank of a family Praethecacinetidae Dovgal, 1996.

A.V. Jankowski (1982) elevated a new family Beckmaniidae with a single genus and species *Beckmania baikalensis* Jankowski, 1982. However, the type species of the genus *Beckmania* Jankowski, 1982 was transferred by the author (Jankowski, 1987) into the genus *Metacineteta* without any comments on the family. Since the type genus was synonymized with *Metacineteta*, the name Beckmaniidae Jankowski, 1982 is a younger synonym of Metacinetidae.

The most complicated situation has probably formed around taxonomy and nomenclature of ectoparasitic exogemmins attaching to the host (ciliates) by single rod-like tentacle. The species with these characters are usually assigned to the family Pseudogemmidae Jankowski, 1978, but various forms from this family reproduce by different modes of budding (Kormos, 1935b, Jankowski, 1981). This generated a need for the assignment of representatives of the family with various modes of budding to the different subclasses. The group of genera with exogemmy must be related to Exogenia respectively.

Semi-circumvaginate budding with lateral protomit position is characteristic of the genera *Pseudogemmides*, *Manuelophrya* and *Mistarcon* (see Chapter 3). The genera must be transferred into Metacinetida Jankowski, 1978 on the basis of these characters. However, rod-like tentacles are characteristic of genera in contrast with other metacinetid

suctorians. Taking these considerations into account, we propose to classify the genera into a separate family. By virtue of the fact that the guide of D. Matthes and others (1988) has gained wide popularity the genus *Manuelophrya* is best known to date. Thus, following the recommendation of 64A of International Code of Zoological Nomenclature (International Code of Zoological Nomenclature, 2000) we indicate *Manuelophrya* Matthes, 1988 as the type genus of the new family. Consequently, the family receives the name Manuelophryidae.

#### FAMILY MANUELOPHRYIDAE DOVGAL, FAM. N.

Suctorians that attach to the host's cell by a single rod-like tentacle or to the host's stalk by a basal protuberance of the stylothecca. There are both loricate (with stylothecca) and unloricate forms. The body is spherical or sac-like in shape. The macronucleus is spherical. Reproduction by exogemmic budding with formation of lateral protomit partially submerged into parental cell (semi-circumvaginate budding). The type genus of the family is *Manuelophrya* Matthes, 1988.

Habitat. Ectoparasites of sessile ciliates.

Within the order Ephelotida Raabe, 1964 we accept only the family Ephelotidae Kent, 1882.

A.V. Jankowski (1978) erected the order Ophryocephalida for small unloricate suctorians with a stalk, a single agile tentacle and reproduction by polyexogemmy. The family Ophryocephalidae Jankowski, 1978 with a single genus *Ophryocephalus* was included into the order by the author. The type species of the genus (*O. capitatus* Wailes, 1925, Fig. 21, G) is the parasite at ephelotid suctorians.

Representatives of the genus *Ophryocephalus* are similar to ephelotid suctorians both in the manner of reproduction and swarmer morphology. It is highly probable that they are ephelotid suctorians specialized to parasitism. Thus, we have no reason to erect a taxon with a high rank. It is expedient to synonymize the name Ophryocephalida Jankowski, 1978 with Ephelotida Raabe, 1964 and Ophryocephalidae Jankowski, 1978 with Ephelotidae Kent, 1882.

A.V. Jankowski (1978) also proposed to unite all unstalked ephelotins into the family Tunicophryidae Jankowski, 1978. However, we not adopt this character as a character of the family. The name Tunicophryidae Jankowski is synonymized with Ephelotidae.

As indicated in Fig. 15, high taxa are separated by the type of the tentacles (in Vermigenia) or by combination of tentacle morphology with presence of the lorica (in thecacinetid suctorians). Consequently, we distinguish the order Spelaeophryida Jankowski, 1978 with capitata tentacles and the order

Ophryodendrida Jankowski, 1975 with rod-like tentacles.

Within order Spelaeophryida the family Spelaeophryidae Batisse, 1975 including stretched forms without actinophores was conserved. The genus *Cucumophrya* Kunz, 1936 is also transferred into this family based on the characters mentioned. The families Lecanophryidae Jankowski, 1973, Dendrosomididae Jankowski, 1981, Dentacinetidae Batisse, 1992 and Thecacinetidae Matthes, 1956 are also included. The name of the order Dendrosomidida Jankowski, 1978 is synonymized with Spelaeophryida Jankowski, 1978.

Within the limits of the order Ophryodendrida Jankowski, 1975 we consider the suctorian family Ophryodendridae Stein, 1867 with characteristic "proboscis-like" actinophores and Rhabdophryidae Jankowski, 1978 with actinophores that are body protuberances or with no actinophores at all.

A.V. Jankowski (1981) described the genus *Crevicometes* and classified it into a new family Crevicometidae Jankowski, 1981 based on the presence of cylindrical actinophore and the absence of the stalk. According to the results of our investigation (Fig. 15), the genus *Crevicometes* falls into a common cluster with ophryodendrid suctorians due to the presence of a typical "ophryodendrid" actinophore. In contrast with A.V. Jankowski's opinion, the genus is unrelated to rhabdophryid suctorians. There are strong grounds for transferring *Crevicometes* into Ophryodendridae. The name Crevicometidae Jankowski, 1981 is a younger synonym of Ophryodendridae respectively.

The family Stylostomatidae was proposed by A. Batisse (1975) for ophryodendrid suctorians with a spindle-like body, apical actinophores and a well-developed stalk. The type genus is *Stylostoma*. The genera *Asterifer* and *Thisarcon* Jankowski, 1981 were also classified into the family. A. Batisse's family was elevated by A.V. Jankowski (1978) to the suborder Stylostomatina Jankowski, 1978. However, suctorians with different types of tentacles and actinophores are found in Stylostomatidae. Moreover, the name *Stylostoma* was synonymized with *Ophryodendron* (see Chapter 3). Consequently, the name Stylostomatidae is synonymized with Ophryodendridae and name Stylostomatina is synonymized with Ophryodendrida.

The family Corethriidae was erected by the author (Jankowski, 1978) for unstalked ophryodendrid suctorians with a disc-like body. Both shape of cell and absence of stalk are at best criteria for a genus and not a family. The name Corethriidae Jankowski, 1978 is a younger synonym of Ophryodendridae.

The ophryodendrids with mucous lorica were classified (Jankowski, 1978) into a separate family Loricodendridae Jankowski, 1978. However, both



family and type genus (*Loricodendron* Jankowski, 1973) proposed by A.V. Jankowski were not accepted by A. Batisse (1994) due to the absence of the lorica in these organisms (there is “pseudolorica” only). In our opinion the presence of mucous lorica is not a good reason for elevation of the ophryodendrid family. The name Loricodendridae is a younger synonym of Ophryodendridae.

The suborder Asteriferina Jankowski, 1978 with a single family Asteriferidae Jankowski, 1978 was proposed by A.V. Jankowski (1978) for suctorians from the genus *Asterifer* with a rosette of 6 flattened actinophores. In our view neither shape nor number of actinophores can serve as criteria of a suborder. The erection of the suborder Ophryodendrina Jankowski, 1978 thus also loses its meaning. The names Asteriferina and Ophryodendrina are synonymized with Ophryodendrida.

The new suborder Nemertodendrina Jankowski, 1981 and family Nemertodendridae Jankowski, 1981 were elevated by A.V. Jankowski (1981) for the genus *Nemertodendron* that had been described by the author earlier (Jankowski, 1978). However, as was noted above we synonymized the generic name. Consequently, Nemertodendrina is a younger synonym of Ophryodendrida and Nemertodendridae is a younger synonym of Ophryodendridae.

As mentioned above, the morphology of adhesive organelles mainly determines the orders in Endogenia. Thus, we distinguish the following orders within the subclass: Acinetida Raabe, 1964 (ciliates attaching by a stalk or stalk-like part of stylothea); Trichophryida Jankowski, 1978 (ciliates attaching to the substrate by body surface or cell protuberance); Endosphaeriida Jankowski, 1978 (with a single family Endosphaeriidae Jankowski, 1978 whose representatives are intracellular and tissue parasites lacking both attaching organelles and tentacles).

In the order Acinetida there are no distinct clusters of loricate and unloricate suctorians (Fig. 16). Thus, we do not accept the suborders Tokophryina Jankowski, 1978 and Acinetina Jankowski, 1978 that were proposed by A.V. Jankowski (1978). It is our opinion that loricate forms must be classified into two families: Acinetidae Ehrenberg, 1838 and Acinetopsidae Jankowski, 1978 (the latter with unique prehensile tentacles). Based on the results of cladistic analysis we transfer the genus *Squalorophrya* Goodrich et Jahn, 1943 with mucous lorica into Acinetidae though the mode of reproduction of these suctorians is still unknown.

It is A.V. Jankowski's (1978) opinion that all endogemmins with mucous lorica must be classified into the family Cryptophryidae Jankowski, 1978. On the contrary, we consider that the mode of lorica is a generic

and not a familial character. The name Cryptophryidae is synonymized with Acinetidae.

We classify the majority of stalked unloricate endogemmins into the family Tokophryidae. *Parastylophrya* is transferred into this family based on the results of phylogenetic analysis. The family Dactylostomatidae Jankowski, 1978 whose representatives possess unusual bottle-like tentacles.

Particular attention must be given to the systematic position of Corynophryidae Jankowski, 1981. The family was erected by A.V. Jankowski (1981) for marine suctorians with sac-like or spherical body, a stalk with an apical widening and exogemmimic budding. In the opinion of A.V. Jankowski, corynophryids are descendants of some representatives of *Paracineta* that lack the lorica. However, this author did not mention his own observations of corynophryid reproduction.

It was correctly indicated by C. Curds (1987) that internal budding was mentioned in the diagnosis of the type genus (*Corynophrya*) of the family (Kahl, 1934). Therefore we transfer Corynophryidae into Acinetida.

As it was indicated above (see Chapter 4), the complex of morphological characters with high taxonomical value is associated with tentacle type. The presence of a unique mode of tentacles is sufficient for erection of taxa with a high rank. In this connection we classify endogemmins with funnel-like tentacles that also isolated in the scheme (Fig. 16) into a separate family Choanophryidae.

#### FAMILY CHOANOPHRIDAE DOVGAL, FAM. N.

Suctorians with unique funnel-like tentacles that lack the inner microtubular layer of the axonema, specialized to feeding on liquid remains of host's food. The macronucleus is spherical or ellipsoid. The type genus of the family is *Choanophrya* Hartog, 1901.

Habitat. Commensals of freshwater crustaceans.

Among unstalked suctorians from the order Trichophryida Jankowski, 1978 sessile and planktonic forms with unramified body stand out. These suctorians are classified into the family Trichophryidae Bütschli, 1879.

We also classify into a separate family Rhynchetidae Jankowski, 1978 parasitic and commensal suctorians with agile tentacles that inhabit freshwater crustaceans. The family is transferred from the order Acinetida into Trichophryida based on the absence of stalk or its homologues. The genus *Riftus* Jankowski, 1981 is also transferred into the Rhynchetidae. In A.V. Jankowski's (1981) opinion this genus is related to tokophryins. However, a distinct affinity between the *Riftus* and *Rhyncheta* escaped the attention of the author.

Consequently, the name Riftidae Jankowski, 1981 is a younger synonym of Rhynchetidae.

Following A.V. Jankowski (1978) we group suctorians that attach to the substrate by an adhesive ring (cinctum or hemicinctum) into the family Erastophryidae Jankowski, 1978.

However, the status of several taxa calls for additional discussion. For example, we do not accept the mode of life as a good reason for erection of an order or a family if it is not associated with any morphological adaptations.

Thus, we synonymize the names Marinectida Jankowski, 1981 and Marinectidae Jankowski, 1978 proposed for planktonic suctorians with Trichophryida Jankowski, 1978 and Trichophryidae Bütschli, 1879 respectively. The presence of symmetrically arranged actinophores (“star-shaped body”) in planktonic trichophryids from the genus *Staurophrya* provides the basis for elevation of a separate family Staurophryidae Jankowski, 1978. In fact the diagnosis of the type genus is consistent with the diagnosis of the family Trichophryidae. The name Staurophryidae is a younger synonym of Trichophryidae.

In our opinion the presence of massive mucous lorica (“heliotheca”) in planktonic forms is a generic and not a familial character. Consequently, the name Mucophryidae Jankowski, 1978 is a younger synonym of Trichophryidae.

A.V. Jankowski (1981) thought that the presence of a special type of tentacles (with a flattened knob) is the principal characteristic of the family Actinobranchiidae Jankowski, 1978. However, it is clear from the data of W. Foissner and others (Foissner et al., 1995) and our observations (Fig. 12) that the flattened knob of capitate tentacle is common among suctorians and can not be used even as a generic character. We synonymize the name Actinobranchiidae with Trichophryidae.

The family of “ichthyophilous trichophryans” was described by A.V. Jankowski (1978) “for small sessile forms with a wide basodisc and from one to two fascicles of the tentacles” and named Caprinianidae Jankowski, 1978. As discussed above, the representatives of the family type genus *Capriniana* attach to the host’s gills by specialized tentacles. However, this character is not sufficient for erection of a family. Thus, the name Caprinianidae Jankowski, 1978 is a younger synonym of Trichophryidae.

The family Peltacinetidae Jankowski, 1981 was erected for small triangular flattened forms with funnel-like tentacles arranged in rows. In A.V. Jankowski’s (1981, p. 85) opinion, the type genus of the family (*Peltacineta* Jankowski, 1978) “...unquestionably is derived from choanophryans”. However, funnel-like

tentacles are not mentioned in the diagnosis of the type species of the genus (*Trichophrya cordiformis* Schewiakoff, 1893; Fig. 25, M) and cannot be seen in W. Schewiakoff’s (1893) figures. Whether or not A.V. Jankowski investigated this species remains unknown. Until the details of tentacle morphology are refined, we conserve the genus *Peltacineta* within Trichophryidae. Consequently, the name Peltacinetidae is synonymized with Trichophryidae.

A.V. Jankowski (1978) also indicated Discosomatellidae Jankowski, 1978 as a separate family within Trichophryida. As discussed above (Chapter 3), we transferred the type genus of the family (*Discosomatella*) into Stylocometidae. This action is supported by cladistic analysis (Fig. 18). The name Discosomatellidae is a younger synonym of Stylocometidae.

The systematic position and taxonomic rank of loricate unstalked suctorians requires a special discussion. The genus *Solenophrya* with a single species *S. crassa* Claparede et Lachmann, 1859 was erected for “unstalked acinetians” (Claparede and Lachmann, 1859). A.V. Jankowski (1981, p. 114) believed that “...the species (*S. crassa*) was redescribed as *Cyclophrya magna* and *Craspedophrya erhardi* at a later time”. In the opinion of this author, E. Claparede and C. Lachmann did not indicate the ramified macronucleus characteristic of the genus *Cyclophrya*. However, in F. Holm’s figure (1925, Fig. 10, p. 399) an ellipsoid macronucleus can be seen in *Solenophrya*. Thus, there is no need to rename Heliophryidae into Solenophryidae Jankowski, 1981 as was proposed by A.V. Jankowski (1981).

Several species that were described as representatives of *Solenophrya* (Penard, 1914, 1920a; Holm, 1925, etc.) are transferred into Metacinetina (Rieder, 1985). Most of the solenophryans described by E. Penard (1914, 1920a) are conserved in the genus (Matthes et al., 1988). The mode of reproduction of these species still unknown, hence we left them in Trichophryida with the rank of the family Solenophryidae. The genus of planktonic loricate endogemmins *Sphaeracineta*, whose systematic position was not indicated by the author (Jankowski, 1987) and two planktonic genera with mucous lorica (*Tetraedrophrya* and *Mucophrya*) are also transferred into the family.

Cladistic analysis brought parasitic loricate endogemmins into a common cluster with *Solenophrya*. The order Pseudogemmida (with the family Pseudogemmidae Jankowski, 1978) was erected by A.V. Jankowski (1978). In his opinion, pseudogemmins are the ancestral group of intracellular parasitic endosphaeriid. In turn, A. Batisse (1994) combined both pseudogemmins and endosphaeriids within the family Endosphaeriidae.

In our view, the hypothesis on the affinity between pseudogemmin and endosphaeriid suctorians is deficient. Contrary to the endosphaeriids, the swimmers of pseudogemmins are similar with trichophryid buds. Thus we believe that pseudogemmin suctorians must be classified within Trichophryida in the rank of the family Pseudogemmidae.

Endogemmin genera with a ramified body fall into a single cluster for which we conserved the family Dendrosomidae Bütschli, 1889. It should be mentioned that A.V. Jankowski (1978) proposed to classify such forms in the order Dendrosomatida Jankowski, 1978 including two suborders: Dendrosomatina Jankowski, 1978 (with a ramified body) and Stylophryina Jankowski, 1978 (with a set of actinophores). In our opinion this is a poor basis for description of taxa of a high rank. The names Dendrosomatida, Dendrosomatina and Stylophryina are synonymized with Trichophryida, whereas the name Stylophryidae Jankowski, 1978 is synonymized with Dendrosomidae.

Subclass Evaginogenia is a suctorian group whose classification was most developed (see Jankowski, 1981). At the same time, the group includes the majority of taxa described by D. Matthes (1954a, 1954b, 1954c, 1954d). Consequently, there are many points to be discussed in connection with this subclass.

There are two distinct groups of genera with different type of tentacles in the scheme of phylogenetical relations (Fig. 18). In our view, they correspond to orders Discophryida Jankowski, 1975 (with capitate tentacles) and Dendrocometida Raabe, 1964 (with rod-like and ramified tentacles).

The order Discophryida was subclassified by A.V. Jankowski (1981) into two suborders: Discophryina Jankowski, 1981 including unloricate forms and Stylocometina Jankowski, 1981 with unstalked sessile forms with rod-like tentacles. However, in our scheme of phylogenetic relations (Fig. 18) the stylocometins are positioned in the cluster adjacent with dendrocometins. Consequently, we transfer the group into Dendrocometida with conservation of the taxonomic rank. Therefore, the elevation of a special suborder for discophryin suctorians loses its meaning. The name Discophryina is a younger synonym of Discophryida Jankowski, 1975.

Within Discophryida we distinguish a family of unloricate inversogemmins with capitate tentacles – Discophryidae Collin, 1912. The family of ectoparasitic suctorians (Rhynchophryidae Jankowski, 1978) with contractile agile tentacles is also applied. The podophrya-like suctorians with anisogamy are classified in the family Prodiscophryidae Jankowski, 1978.

The family Coronodiscophryidae Jankowski, 1981 was proposed for discophryins with unflattened body

and basally placed tentacles but the name of the type genus was synonymized in Chapter 3. Thus, we believe that the name Coronodiscophryidae is a younger synonym of Discophryidae Collin, 1912.

The same is true for the families Multifasciculatidae Jankowski, 1981 with isolated apical and lateral fascicles of tentacles and Cyathodiscophryidae Jankowski, 1981 with semilorica. The type genus of the former family *Multifasciculatum* Goodrich et Jahn, 1943 was synonymized with *Discophrya* by D. Matthes and others (1988), whereas the type genus of the latter (*Cyathodiscophrya*) was synonymized with *Discophrya* in Chapter 3 of this work. Consequently, the names Multifasciculatidae and Cyathodiscophryidae are synonymized with Discophryidae Collin, 1912.

All genera of loricate discophryins are classified into the family Periacinetidae Jankowski, 1978.

A separate family Caracatharinidae Jankowski, 1981 was erected by A.V. Jankowski (1981) for loricate suctorians with a single apical fascicle of tentacles and a ribbon-like or ramified macronucleus. However, the number of tentacle fascicles is unsuitable as a criterion of the family. The name Caracatharinidae Jankowski, 1981 is a younger synonym of Periacinetidae.

The new order Heliophryida was elevated by A.V. Jankowski (1981) for disc-like, spread upon the substrate suctorians with clavate tentacles. It is evident from Fig. 18 that such forms are positioned into a common group with discophryins. In fact, the heliophryins attach to the substrate not by “special secretion” as A.V. Jankowski (1981) claimed but by a wide adhesive disc which is a modified stalk (Batisse, 1994). This suggests an affinity between heliophryids and discophryids. Thus, we conserve the family Heliophryidae within the order Discophryida. The name Heliophryida is synonymized with Discophryida.

In the order Dendrocometida Raabe, 1964 A.V. Jankowski (1978) distinguished two families (Dendrocometidae and Cometodendridae Jankowski, 1978) or (Jankowski, 1981), one family with two subfamilies. However, the suborder Stylocometina was transferred into Dendrocometida. Thus, the forms with ramified tentacles must be classified into another suborder Dendrocometina.

#### **SUBORDER DENDROCOMETINA DOVGAL, SUBORD. N. (NON RAABE, 1964 IN BATISSE, 1994)**

Hemispherical, disc-like, spread over substrate or vase-like unstalked suctorians. The adhesion to the substrate is by means of the basal body protuberance or a tectinous adhesive disc which is a modified stalk. The macronucleus is spherical or ellipsoid. The presence of

ramified tentacles is the key characteristic of the suborder.

The species of anaerobic ciliates *Enchelyomorpha vermicularis* (Smith, 1899) (Fig. 29, I) was earlier assigned to actinobolins (with the rank of the family Enchelyomorphidae) based on the pattern of ciliature and presence of the tentacles.

However, electron microscopical investigation has shown (Foissner and Foissner, 1995, Foissner et al., 1995) that in the tentacle of *E. vermicularis* there are a microtubular axonema and haptocysts characteristic for suctorians.

First W. Foissner and others (1995) considered the species in question as a swarmer of an unidentified suctorian. The trophonts and initial stages of budding of the species were investigated (Foissner and Foissner, 1995).

Although there is some similarity in anlage of protomits in enchelyomorphs and cyathodiniids (Foissner and Foissner, 1995) the data available are insufficient to state that the reproduction of *Enchelyomorpha* corresponds to inversogemmy. Similarity between swarmers of *E. vermicularis* and *Parapodophrya* in our view is associated with parallelism in larval adaptations.

The swarmer of *Enchelyomorpha* is an example of high specialization to anaerobic conditions. Similar to most anaerobic protists, lack of mitochondria and presence of hydrogenosomes and autophagous vacuoles are characteristic for enchelyomorphs. It is possible that mutualism with bacteria allows the swarmer to have a longer life than that of trophont. Abundant observations of migratory stages and only rare records of trophonts indirectly point to this. Additional investigations on the morphology and life cycle of this suctorian ciliate are necessary to clarify its systematic position. For the present we place Enchelyomorphidae into the suborder Stylocometina based on the results of phylogenetic analysis.

The systematic position of the genus *Echinophrya* with unknown mode of budding has been obscure for a long time. B. Swarczewsky (1928c) thought that the genus is related to discophryins. However, the genus was found in a common cluster with *Stylocometes* in cladistic analysis. Thus, *Echinophrya* is transferred into Stylocometidae Jankowski, 1978.

Thus we distinguish two suborders within the order Dendrocometida: Stylocometina Jankowski, 1981 with the families Stylocometidae Jankowski, 1981 and Enchelyomorphidae Augustin et Foissner, 1992 and Dendrocometina subord. n. with the families Dendrocometidae Stein, 1851 and Cometodendridae Jankowski, 1978.

The systematic position and taxonomical rank of suctorian commensals of guinea pigs intestine (genus

*Cyathodinium*) calls for a special discussion. Contrary to the other suctorians, cyathodiniid possess ciliature throughout the life cycle. A variety of inversogemmy with simultaneous formation of two protomits is also characteristic of the group (Paulin et al., 1969).

A.V. Jankowski (1975) proposed to classify cyathodiniids into the order with an unclear systematic position and later (Jankowski, 1978) into the subclass Neotenea with a short diagnosis: "neotenic forms from the intestine of guinea pigs (*Cavia*) that feed and divide at the stage of tomit".

A. Batisse (1994) in turn placed the family Cyathodiniidae da Cunha, 1914 into the suborder Discophryina Batisse, 1957 based on the characteristics of their budding.

As noted above, we do not accept A.V. Jankowski's subclass. However, the combination of characters makes us classify the group in the rank of the order Cyathodiniida within Evaginogenia.

The systematic position of the endoparasites of rotifers from the genus *Tripanococcus* invites further investigation. A.V. Jankowski (1981) placed the genus into Endosphaeriida. A. Batisse (1994) discussed the genus within the family Discophryidae based on the presence of inversogemmy investigated by Penard (1920b).

In our opinion there is a reason for transferring the *Tripanococcus* into Evaginogenia. However, the representatives of the genus possess several unique characteristics such as reduction of tentacles and the mode of inversogemmy. We believe that on the strength of these arguments *Tripanococcus* must be classified in a taxon with a rank equal to that of convergently similar endosphaeriids. Therefore we erect a new order Tripanococcina ord. n. and family Tripanococcidae fam. n.

#### ORDER TRIPANOCOCCINA DOVGAL, ORD. N.

Suctorian ciliates that lack tentacles, stalk and lorica. The body is sac-like. Swarmers ellipsoid, flattened laterally and with a few longitudinal kineties. Reproduction by sequential polyinversogemmy is characteristic of the group. The order includes one family Tripanococcidae Dovgal, fam. n. (with characteristics of the order). The type genus of the family is *Tripanococcus* Stein, 1867.

Habitat. Parasites of tissue of freshwater rotifers.

Thus, as a result of systematic revision we accept the subdivision of the class Suctorea into four subclasses with 15 orders, 2 suborders, 41 families and 124 genera. The summarised classification is presented below.

#### CLASS SUCTOREA CLAPAREDE ET LACHMANN, 1859

Ciliates lacking cytostome but with from several to many tentacles (rarely no tentacles). The tentacles have

an axonema with two layers of microtubules and a special kind of extrusomes – haptocysts. Cilia are absent in trophonts (though there is infraciliature). There are contractile vacuoles but no cytoproct. Migratory stages are produced by different modes of budding and generally bear ciliature. Conjugation by both isogamy and anisogamy. The body shape varies from spherical to ramified. The cells often have a non-contractile stalk produced by scopuloid. The size of body from 10 to 5000 µm. Commensals or parasites of various water animals (mostly invertebrates) and plants; fouling organisms; plankters. There are also endocommensals of digestive tract of Equidae, Caviidae, Proboscidea and Rhinocerotidae.

**SUBCLASS EXOGENIA COLLIN, 1912**

The suctorians reproducing by exogenous (monogemmimic or polygemmic) budding or by binary fission. As a rule, migratory stages are ciliary (except *Phalacroleptes*). Trophont stages are often stalked, loricate or unloricate.

**ORDER PODOPHRYIDA JANKOWSKI, 1967**

= Allantosomatida Jankowski, 1978 syn. n.

Small, pyriform or spherical suctorians with tentacles evenly distributed or (rarely) arranged in fascicles. Actinophores are absent. The stalk usually present, except in planktonic forms or symbionts of mammal intestine. Reproduction by binary fission or monogemmimic budding.

**FAMILY PODOPHRYIDAE BÜTSCHLI, 1889**

Suctorians with spherical or sac-like body, tentacles evenly distributed or (rarely) arranged in fascicles. Actinophores absent. The stalk usually present, but trophonts of several species lack adhesive organelles. Tentacles are capitate, rarely with basal widenings. Reproduction by monogemmimic exogemmy with formation of apical protomit. The binary fission is also present. Swarmer unflattened and with tentacles. A stalked cyst with transverse circular ribs is characteristic of the representatives of the family.

Habitat. Sessile and planktonic forms, also parasites of other ciliates.

1. *Podophrya* Ehrenberg, 1834

*Podophrya fixa* (O.F. Müller, 1786) (Type species - T.S., Fig. 19, B), *P. benedeni* Fraipont, 1877, *P. bengalensis* Ghosh, 1929, *P. brevipoda* Sand, 1899, *P. comosa* Penard, 1920, *P. fallax* Dingfelder, 1961, *P. globulifera* Kahl, 1931, *P. gracilis* Calkins, 1902, *P. halophila* Kahl, 1934, *P. hungarica* K. Kormos, 1961,

*P. libera* Perty, 1852, *P. macrostyla* Stokes, 1885, *P. poculum* Allmann, 1875, *P. sandi* Collin, 1912.

2. *Parapodophrya* Kahl, 1931

*Parapodophrya soliformis* (Lauterborn, 1901) (T.S., Fig. 19, A), *P. atypica* Gonnert, 1935, *P. denticulata* Kahl, 1931, *P. nigricans* Kahl, 1931, *P. palmigera* (Penard, 1920), *P. sparganium* Kahl, 1931, *P. typha* Kahl, 1931.

3. *Sphaerophrya* Claparede et Lachmann, 1859

*Sphaerophrya magna* Maupas, 1881 (T.S., Fig. 19, C), *S. amoeboides* (Sand, 1899) comb. n. for *Trichophrya amoeboides* Sand, 1899, *S. canelli* Clement-Iftode, 1967, *S. doliolum* Penard, 1920, *S. epizoica* (Hammann, 1952) comb. n. for *Podophrya epizoica* Hammann, 1952, *S. grelli* Diekmann, 1985 comb. n. for *Podophrya grelli* Diekmann, 1985, *S. hydrostatica* Engelmann, 1878, *S. iftodi* (Curds, 1986) comb. n. for *P. iftodi* Curds, 1986, *S. insolita* (Jankowski, 1973), *S. mamillata* Oppenheim, 1976, *S. natans* Penard, 1920, *S. ovata* (Weisse, 1847), *S. parameciorum* Maupas, 1881, *S. parasitica* (Faure-Fremiet, 1945) comb. n. for *P. parasitica* Faure-Fremiet, 1945, *S. parurolepti* Foissner, 1980, *S. pusilla* Claparede et Lachmann, 1859, *S. sol* Metschnikoff, 1864, *S. stentoris* Maupas, 1881, *S. stokesii* Mamaeva, 1979, *S. terricola* Foissner, 1986, *S. urostylae* (Maupas, 1881).

**FAMILY ALLANTOSOMATIDAE JANKOWSKI, 1978**

Suctorians with a sac-like unflattened body. Capitate or rod-like tentacles are arranged in fascicles or rows at the poles of body or are evenly distributed. There are additional folds of the tentacle axonema. Reproduction by binary fission.

Habitat. Endocommensals of digestive tract of mammals (Equidae, Proboscidea and Rhinocerotidae).

1. *Allantosoma* Gassovsky, 1918

*Allantosoma intestinalis* Gassovsky, 1918 (T.S., Fig. 19, E and Fig. 8, A), *A. cucumis* Strelkow, 1939.

2. *Allantoxena* Jankowski, 1978

*Allantoxena biserialis* (Strelkow, 1939) (T.S., Fig. 19, G), *A. japonensis* (Imai, 1979).

3. *Arcosoma* Jankowski, 1967

*Arcosoma dicorniger* (Hsiung, 1928) (T.S., Fig. 19, F), *A. brevicorniger* (Hsiung, 1928), *A. lineare* (Strelkov, 1939).

4. *Vanhovenia* Dovgal, gen. n.

*Vanhovenia multisuctores* (Van Hoven et al., 1998) (T.S., Fig. 19, D) comb. n. for *Allantosoma multisuctores* Van Hoven et al., 1998.

**FAMILY SEVERONIDAE JANKOWSKI, 1981**

Suctorians with a spherical body attaching to the substrate by protuberances on the basal body surface.

Capitate tentacles with wide basal parts and well-developed knobs are evenly distributed on the apical body surface.

Habitat. Ectocommensals of marine sponges.

1. *Severonis* Jankowski, 1981

*Severonis spongiarum* Jankowski, 1981 (T.S., Fig. 19, H).

#### ORDER PHALACROCLEPTIDA JANKOWSKI, 1978

Suctorians with a small body of flattened hemispherical shape, with neither cilia nor infraciliature at all stages of life cycle. There are very short tentacles that serve for attachment. Reproduction by binary fission.

#### FAMILY PHALACROCLEPTIDAE KOZLOFF, 1966

With characteristics of the order.

Habitat. Parasitic on polychaete annelids.

1. *Phalacrocleptes* Kozloff, 1966

*Phalacrocleptes verruciformis* Kozloff, 1966 (T.S., Fig. 19, I and Fig. 8, B).

#### ORDER METACINETIDA JANKOWSKI, 1978

= Paracinetida Jankowski, 1978 syn.n.

= Urnulida Jankowski, 1978 syn. n.

Usually loricate suctorians with a spherical or sac-like body. Capitate (rarely rod-like) tentacles arranged in fascicles or rows on the apical body surface. Reproduction by exogemmic, mainly semi-circumvaginative budding.

#### FAMILY METACINETIDAE BÜTSCHLI, 1889

= Urnulidae Fraipont, 1878 syn.n.

= Beckmaniidae Jankowski, 1982 syn. n.

Suctorians with a spherical body attached to the edge of apical opening of the stylothea. The aperture of the lorica often with cuts. Capitate tentacles are single or arranged in fascicles or rows. Reproduction is by semi-circumvaginative budding with laterally positioned protomit. Swimmers are ovoid with spiral ciliary rows.

Habitat. Representatives live on inanimate substrates, water invertebrates and plants and as parasites of other ciliates.

1. *Metacineteta* Bütschli, 1889

= *Discacineteta* Jankowski, 1981 syn. n.

*Metacineteta mystacina* (Ehrenberg, 1831) (T.S., Fig. 19, J), *M. acuminata* Stokes, 1887, *M. angularis* (Maskell, 1887), *M. baikalensis* (Jankowski, 1982), *M. flos* (Maskell, 1887), *M. longipes* (Mereschkowsky, 1877), *M. macrocaulis* (Stokes, 1887), *M. micraster* (Penard, 1914), *M. rossica* (Jankowski, 1981), *M. stagnatilis* (Stokes, 1886), *M. yoshii* Nozawa, 1938.

2. *Urnula* Claparede et Lachmann, 1861

*Urnula epistylidis* Claparede et Lachmann, 1861 (T.S., Fig. 19, K), *U. turpissima* Kormos K., 1958.

#### FAMILY PARACINETIDAE JANKOWSKI, 1978

Suctorians usually with a spherical or sac-like body. The opening of the stylothea without notches. Tentacles capitate, arranged into a single apical fascicle or row. Reproduction by regular exogemmic or semi-circumvaginative budding with formation of apical protomit.

Habitat. Representatives live in soil, on inanimate substrates, marine and freshwater invertebrates and plants.

1. *Paracineteta* Collin, 1912

= *Miracineteta* Jankowski, 1981 syn. n.

= *Flectacineteta* Jankowski, 1978 syn. n.

= *Faltacineteta* Jankowski, 1981 syn. n.

*Paracineteta patula* (Claparede et Lachmann, 1861) (T.S., Fig. 19, L), *P. dadayi* Kahl, 1934, *P. divisa* (Fraipont, 1877), *P. gaetani* Sewell, 1951, *P. hawniensis* (Ehrenberg, 1838), *P. irregularis* Dons, 1927, *P. jorisi* (Sand, 1895), *P. karanakarani* Santhakumari, 1986, *P. lineata* Jones, 1973, *P. livadiana* (Mereschkowsky, 1881), *P. meridionalis* Jones, 1973, *P. moebiusi* Kahl, 1934, *P. neapolitana* (Daday, 1886), *P. saifulae* (Mereschkowsky, 1877), *P. scanica* Allgen, 1934, *P. scottocalani* (Sewell, 1951), *P. stresemanni* Allgen, 1951, *P. trichophora* (Allgen, 1951) comb. n. for *Thecacineteta trichophora* Allgen, 1951, *P. tuba* (Zelinka, 1914), *P. vorticelloides* (Fraipont, 1877), *P. anisostyla* (Fernandez-Leborans et al., 1996) comb. n. for *Corynophrya anisostyla* Fernandez-Leborans et al., 1996.

2. *Actinocyathula* Corliss, 1960

*Actinocyathula cidaris* (Kent, 1882) (T.S., Fig. 19, M), *A. crenata* (Fraipont, 1877), *A. diadema* (Collin, 1912), *A. homari* (Sand, 1899), *A. pleuromammae* (Steuer, 1928).

3. *Limnoricus* Jankowski, 1981

= *Deltacineteta* Jankowski, 1981 syn. n.

*Limnoricus ceter* Jankowski, 1981 (T.S., Fig. 20, A), *L. seticolus* (Jankowski, 1981) comb. n. for *Deltacineteta seticola* Jankowski, 1981.

4. *Distarcon* Jankowski, 1987

*Distarcon emeritae* (Small et Lynn, 1985) (T.S., Fig. 20, B).

5. *Loricophrya* Matthes, 1956

*Loricophrya parva* (Schulz, 1932) (T.S., Fig. 20, E), *L. sacculus* (Penard, 1914) comb. n. for *Solenophrya sacculus* Penard, 1914, *L. bifaria* (Stokes, 1887), *L. caepula* (Penard, 1920), *L. lauterborni* (Sondheim, 1929), *L. multitentaculata* (Sand, 1895), *L. oviformis* (Dons, 1918), *L. sivertseni* (Allgen, 1951), *L. solenophryaformis* (Sand, 1899).

6. *Luxophrya* Jankowski, 1978

*Luxophrya limbata* (Maupas, 1881) (T.S., Fig. 20, D), *L. maupasi* (Bütschli, 1889) comb. n. for *Podophrya maupasi* Bütschli, 1889.

7. *Nipponarcon* Jankowski, 1981

*Nipponarcon setarius* Jankowski, 1981 (T.S., Fig. 20, C).

**FAMILY PRAETHECACINETIDAE DOVGAL, 1996**

Suctorian ciliates with a pyriform or sac-like stalked body attached to the bottom of the lorica. Capitulate tentacles are arranged in a single apical fascicle. Reproduction by exogemmy with formation of laterally positioned elongated ciliary protomit.

Habitat. Commensals of marine invertebrates.

1. *Praethecacineta* Mathes, 1956

*Praethecacineta halacari* (Schulz, 1933) (T.S., Fig. 20, F).

**FAMILY MANUELOPHRYIDAE DOVGAL, FAM. N.**

With the above diagnosis.

1. *Manuelophrya* Matthes, 1988

*Manuelophrya hanna* (Guhl, 1985) (T.S., Fig. 20, I).

2. *Pseudogemmides* Kormos, 1935

*Pseudogemmides globosa* Kormos, 1935 (T.S., Fig. 20, H and Fig. 7, Db).

3. *Mistarcon* Jankowski, 1986

*Mistarcon parasiticus* (Nozawa, 1939) (T.S., Fig. 20, G).

**ORDER TACHYBLASTONIDA JANKOWSKI, 1978**

Parasitic suctorians with two alternate generations. One generation, loricate and attached to host, produces several (up to 16) bottle-like unciliary swarmers which pierce the pellicle of another host (ciliate). The other generation lives parasitically in the host's cytoplasm and produces large ciliated swarmers, which become loricate after adhesion. Both types of protomits are laterally positioned. Reproduction by sequential semi-circumvaginate budding.

**FAMILY TACHYBLASTONIDAE GRELL, 1970**

With characteristics of the order.

Habitat. The loricate generation lives on various marine hydrobionts, whereas the trophont stage lives within the cytoplasm of suctorians (*Ephelota* sp.).

1. *Tachyblaston* Martin, 1909

*Tachyblaston ephelotensis* Martin, 1909 (T.S., Fig. 20, J).

**ORDER EPHELOTIDA RAABE, 1964**

= Ophryocephalida Jankowski, 1978 syn. n.

Marine suctorians with large truncate-spherical adults that possess both regular sucking tentacles and additional prehensile tentacle-like organelles. The latter may be absent in parasitic forms. The stalk (rarely lorica) usually present. The macronucleus is usually ramified (crown-like). Reproduction is by synchronous polyexogemmy. Swarmers are ellipsoidal and flattened, with horseshoe-shaped main ciliary field.

**FAMILY EPHELOTIDAE KENT, 1882**

= Ophryocephalidae Jankowski, 1978 syn. n.

= Tunicophryidae Jankowski, 1978 syn. n.

With characteristics of the order.

Habitat. Commensals of various marine invertebrates or fouling organisms.

1. *Ephelota* Wright, 1859

= *Sargassephelota* Jankowski, 1981 syn. n.

= *Discephelota* Jankowski, 1981 syn. n.

*Ephelota gemmipara* (Hertwig, 1875) (T.S., Fig. 21, A), *E. butschliana* Ishikawa, 1896, *E. coronata* Kent, 1881, *E. cothurnata* Dons, 1915, *E. crustaceorum* (Haller, 1880), *E. dalyelli* Holt, 1891, *E. gigantea* Noble, 1929, *E. lacazei* (Gourret et Roeser, 1887), *E. mammilata* Dons, 1915, *E. microsoma* (Maupas, 1881), *E. minima* Noble, 1929, *E. neglecta* Sand, 1899, *E. plana* Wailes, 1925, *E. pusilla* (Koch, 1876), *E. suzukiensis* Yagiu, 1980, *E. thouleti* (Maupas, 1881), *E. truncata* (Fraipont, 1878).

2. *Metephelota* Willis, 1945

*Metephelota coronata* Willis, 1945 (T.S., Fig. 21, C), *M. excavata* (Dons, 1938) comb. n. for *Podocyathus excavatus* Dons, 1938.

3. *Podocyathus* Kent, 1881

*Podocyathus diadema* Kent, 1881 (T.S., Fig. 21, D), *P. paguri* Zhadan et Mikrjukov, 1996.

4. *Shellephelota* Jankowski, 1981

*Shellephelota branchialis* Jankowski, 1981 (T.S., Fig. 21, E).

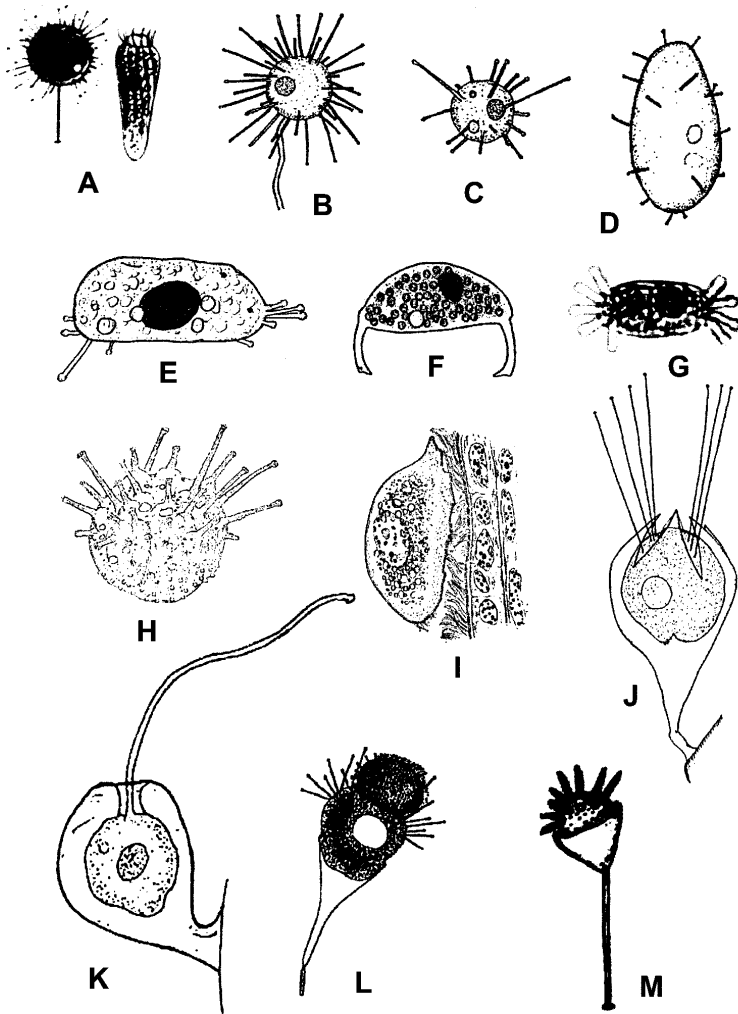


Fig. 19. Type species of the podophryid, phalacrocleptid and metacinetid suctorian genera. A – *Parapodophrya soliformis* (Lauterborn, 1901), from Kahl, 1931; B – *Podophrya fixa* (Muller, 1786), orig.; C – *Sphaerophrya magna* Maupas, 1881, orig.; D – *Vanhovenia multisuctores* (Van Hoven et al., 1998), from Van Hoven et al., 1998; E – *Allantosoma intestinalis* Gassowski, 1918, orig.; F – *Arcosoma dicorniger* (Hsiung, 1928), from Kudo, 1946; G – *Allantoxena biserialis* (Strelkow, 1939), from Ike et al., 1983; H – *Severonis spongiarum* Jankowski, 1981, from Jankowski, 1981; I – *Phalacrocleptes verruciformis* Kozloff, 1966, from Jankowski, 1981; J – *Metacineta mystacina* (Ehrenberg, 1831), orig.; K – *Urnula epistylidis* Claparede et Lachmann, 1861, orig.; L – *Paracineta patula* (Claparede et Lachmann, 1861), budding, from Collin, 1912; M – *Actinocyathula cidaris* (Kent, 1882), from Kahl, 1934.

5. *Thaumtophrya* Collin, 1912  
*Thaumtophrya troid* (Claparede et Lachmann, 1859) (T.S., Fig. 21, F).
6. *Tunicophrya* Jankowski, 1973  
*Tunicophrya sessilis* (Collin, 1912) (T.S., Fig. 21, B).
7. *Ophiurephelota* Jankowski, 1981  
*Ophiurephelota tenax* Jankowski, 1981 (T.S., Fig. 21, H).
8. *Ophryocephalus* Wailes, 1925  
*Ophryocephalus capitatus* Wailes, 1925 (T.S., Fig. 21, G).

**SUBCLASS VERMIGENIA JANKOWSKI, 1978**

Suctorians with vermigemmic budding producing large, vermiform unciliary swarms.

**ORDER SPELAEOPHRYIDA JANKOWSKI, 1978**

= Dendrosomidida Jankowski, 1978 syn. n.

Vermigemmin suctorians with a bowl-like or stretched, rarely ramified body, usually with a stalk. Lorica is absent. Tentacles are capitata and positioned on the apical or lateral body surface, in fascicles or rows.

**FAMILY SPELAEOPHRYIDAE BATISSE, 1975**

Freshwater and marine suctorians with cylindrical or conical body. Capitata tentacles are arranged in an apical corona or in groups along the body. There is a short stalk.

Habitat. Commensals of marine and freshwater crustaceans.

1. *Spelaeophrya* Stammer, 1935  
*Spelaeophrya polypoides* (Daday, 1907) (T.S., Fig. 21, I).
2. *Cucumophrya* Kunz, 1936  
*Cucumophrya leptomesochrae* Kunz, 1936 (T.S., Fig. 22, B).



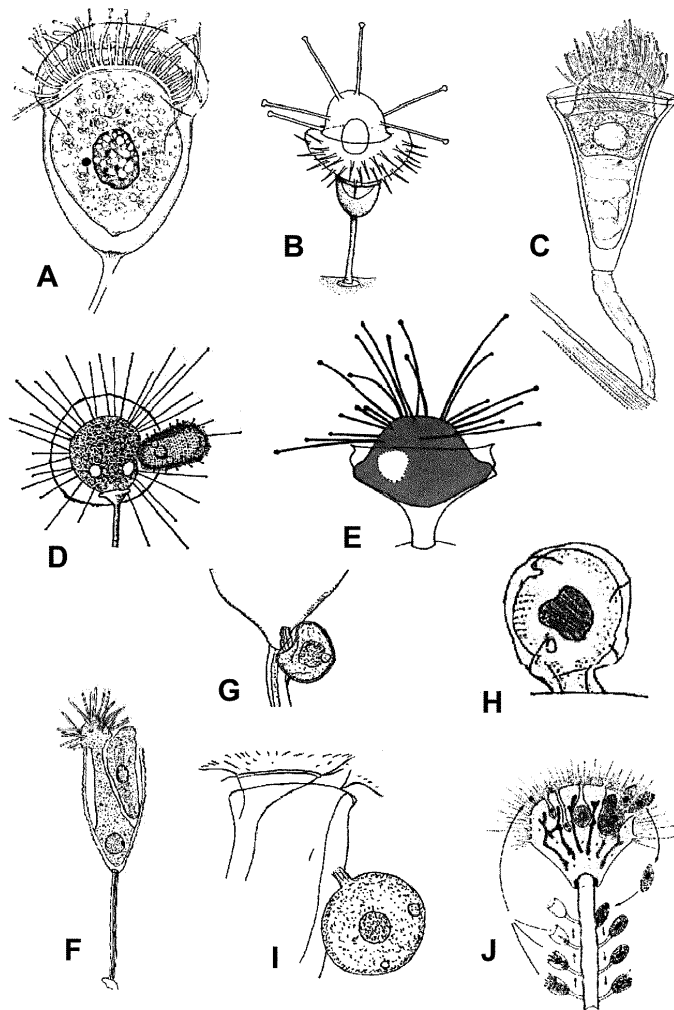


Fig. 20. Type species of the metacinetid and tachyblastonid suctorian genera. A – *Limnoricus ceter* Jankowski, 1981, from Jankowski, 1981; B – *Distarcon emeritae* (Small et Lynn, 1985), from Small and Lynn, 1985; C – *Nipponarcon setarius* Jankowski, 1981, from Jankowski, 1981; D – *Luxophrya limbata* (Maupas, 1881), budding, from Collin, 1912; E – *Loricophrya parva* (Schulz, 1932), from Curds, 1987; F – *Praethecacineta halacari* (Schulz, 1933), budding, from Matthes et al., 1988; G – *Mistarcon parasiticus* (Nozawa, 1939), orig.; H – *Pseudogemmides globosa* Kormos, 1935, budding, orig.; I – *Manuelophrya hanna* (Guhl, 1985), orig.; J – *Tachyblaston ephelotensis* Martin, 1909, life cycle, from Grell, 1950.

**FAMILY LECANOPHRYIDAE JANKOWSKI, 1973**

Suctorians with a cup-like or laterally flattened body. Tentacles are capitata with basal widenings, arranged in rows on the apical body surface or in fascicles on the actinophores. There is a stalk.

Habitat. Commensals of brackish-water and freshwater harpacticoid crustaceans.

1. *Lecanophrya* Kahl, 1934

*Lecanophrya drosera* Kahl, 1934 (T.S., Fig. 21, J), *L. truncata* (Collin, 1909), *L. crassimarginata* Kahl, 1934.

2. *Lecanophryella* Dovgal, 1985

*Lecanophryella paraleptastaci* Dovgal, 1985 (T.S., Fig. 21, K), *L. satyanandani* (Santhakumari, 1986).

**FAMILY DENDROSOMIDIDAE JANKOWSKI, 1981**

Suctorians with a ramified body or well-developed actinophores. Capitata tentacles are arranged in fascicles or rows on the branches of the body. The macronucleus is ramified, ribbon-like or spherical.

Habitat. Ectocommensals of marine crustaceans.

1. *Dendrosomides* Collin, 1906

= *Stylogemma* Jankowski, 1981 syn. n.

*Dendrosomides paguri* Collin, 1906 (T.S., Fig. 21, L), *D. grassei* Batisse, 1986, *D. wailesi* (Kahl, 1934) comb. n. for *Rhabdophrya wailesi* Kahl, 1934.

2. *Rodosomides* Jankowski, 1981

*Rodosomides lucicutiae* (Bowman, 1977) (T.S., Fig. 22, A).

3. *Asterifer* Jankowski, 1967

*Asterifer faurei* (Guilcher, 1950) (T.S., Fig. 22, C).

4. *Leboransia* Dovgal gen. n.

*Leboransia mysidacea* (Fernandez-Leborans et al., 1996) (T.S., Fig. 22, D) comb. n. for *Ophryodendron mysidacii* Fernandez-Leborans et al, 1996.

**FAMILY DENTACINETIDAE BATISSE 1992**

Stalked suctorians with unflattened body bearing characteristic longitudinal cortical ribs. Tentacles are clavate and agile, arranged in a single apical fascicle.

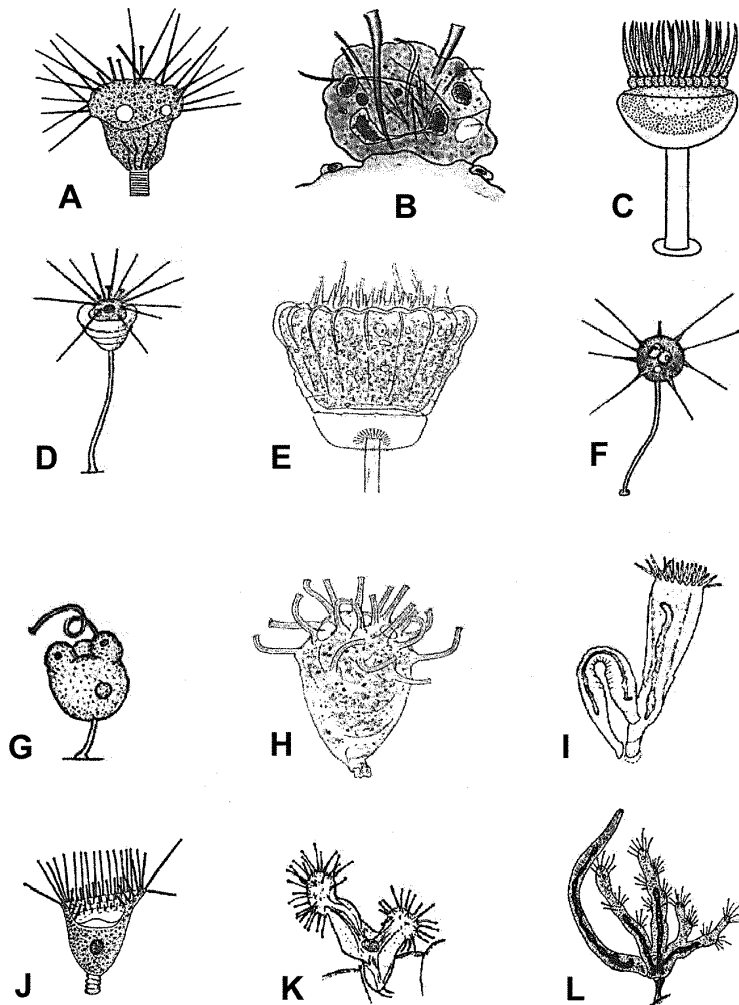


Fig. 21. Type species of the ephelotid and spelaeophryid suctorian genera. A – *Ephelota gemmipara* (Hertwig, 1875), from Collin, 1912; B – *Tunicophrya sessilis* (Collin, 1912), from Collin, 1912; C – *Metephelota coronata* Willis, 1945, from Willis, 1945; D – *Podocyathus diadema* Kent, 1881, from Kudo, 1946; E – *Shellephelota branchialis* Jankowski, 1981, from Jankowski, 1981; F – *Thaumatophrya troid* (Claparede et Lachmann, 1859), from Kudo, 1946; G – *Ophryocephalus capitatus* Wailes, 1925, from Kudo, 1946; H – *Ophiurephelota tenax* Jankowski, 1981, from Jankowski, 1981; I – *Spelaeophrya polypoides* (Daday, 1907), budding, from Matthes et al., 1988; J – *Lecanophrya drosera* Kahl, 1934, from Kahl, 1934; K – *Lecanophryella paraleptastaci* Dovgal, 1985, orig.; L – *Dendrosomides paguri* Collin, 1906, budding, from Collin, 1912.

Habitat. Ectocommensals of marine harpacticoid crustaceans.

1. *Dentacineta* Jankowski, 1978  
= *Dentacinetides* Batisse, 1992 syn. n.  
*Dentacineta campanuliformis* (Collin, 1909) (T.S., Fig. 22, E), *D. collini* (Batisse, 1992) comb. n. for *Dentacinetides collini* Batisse, 1992.
2. *Pleurophryodendron* Jankowski, 1978  
*Pleurophryodendron reversum* (Collin, 1909) (T.S., Fig. 22, F).

**FAMILY THECACINETIDAE MATTHES, 1956**

Suctorians with a sac-like, stalked, loricate body with apically grouped clavate tentacles. Reproduction by vermigemmy with formation of lateral, vermiform protomit.

Habitat. Ectocommensals of marine crustaceans, nematodes and algae.

1. *Thecacineta* Collin, 1909  
= *Lissacineta* Jankowski, 1981 syn. n.  
= *Litacineta* Jankowski, 1978 syn. n.  
= *Paradentacineta* Jankowski, 1978 syn. n.  
*Thecacineta calix* (Schroder, 1901) (T.S., Fig. 22, G), *T. allgeni* (Jankowski, 1981) comb. n. for *Lissacineta allgeni* Jankowski, 1981, *T. cattanei* (Parona, 1883), *T. contorta* (Moebius, 1888), *T. cothurnioides* Collin, 1909, *T. cypridinae* Collin, 1912, *T. desmodorae* Schulz, 1931, *T. donsi* Allgen, 1935, *T. edmondsoni* King, 1932, *T. gracilis* Wailes, 1928, *T. inclusa* (Meunier, 1910), *T. laophontis* Jankowski, 1981, *T. lasanicola* (Maskell, 1887), *T. longepetiolata* Allgen, 1951, *T. microsetellis* Jankowski, 1981, *T. oblonga* Allgen, 1955, *T. oregonensis* Murphy, 1963, *T. paradesmodorae* Allgen, 1950, *T. simplex* (Maskell, 1886), *T. speciosa* Maskell, 1886, *T. spirinae* Allgen, 1934, *T. subantarctica* Allgen, 1950, *T. tulipa* (Maskell, 1887).

**ORDER OPHRYODENDRIDA JANKOWSKI, 1975**

- = Stylostomatina Jankowski, 1978 syn. n.
- = Asteriferina Jankowski, 1978 syn. n.
- = Ophryodendrina Jankowski, 1978 syn. n.
- = Nemertodendrina Jankowski, 1981 syn. n.

Marine suctorians with a sac-like, unflattened or laterally flattened body. The key characteristic of the order is the presence of the rod-like (rarely ramified) tentacles positioned on the actinophores or the body surface. There are loricate and unloricate forms attaching to the substrate by the stalk or the surface of the body.

**FAMILY OPHRYODENDRIDAE STEIN, 1867**

- = Crevicometidae Jankowski, 1981 syn. n.
- = Stylostomatidae Batisse, 1975 syn. n.
- = Corethriidae Jankowski, 1978 syn. n.
- = Loricodendridae Jankowski, 1978 syn. n.
- = Nemertodendridae Jankowski, 1981 syn. n.

Suctorians with rod-like or ramified tentacles positioned on one or more extensible proboscis-like actinophores or (rarely) also on the body. There are loricate, unloricate, stalked and unstalked species.

Habitat. Ectocommensals of marine invertebrates, mostly crustaceans.

1. *Ophryodendron* Claparede et Lachmann, 1859 = *Stylostoma* Milne, 1886 syn. n.  
= *Thisarcon* Jankowski, 1981 syn. n.  
= *Elitarcon* Jankowski, 1981 syn. n.  
= *Nemertodendron* Jankowski, 1978 syn. n.  
= *Stylophryodendron* Jankowski, 1978 syn. n.  
= *Setarcon* Jankowski, 1981 syn. n.  
= *Isopodarcon* Jankowski, 1981 syn. n.  
= *Syllarcon* Jankowski, 1981 syn. n.  
*Ophryodendron abietinum* Claparede et Lachmann, 1859 (T.S., Fig. 22, H), *O. annulatorum* Saint Joseph, 1886, *O. belgicum* Fraipont, 1878, *O. conicum* Schroder, 1907, *O. draconematis* (Jankowski, 1981) comb. n. for *Syllarcon draconematis* Jankowski, 1981, *O. forrestii* (Milne, 1886) comb. n. for *Stylostoma forrestii* Milne, 1886, *O. harmothois* (Jankowski, 1981) comb. n. for *Elitarcon harmothois* Jankowski, 1981, *O. macquariae* Johnston, 1938, *O. multicapitatum* Kent, 1881, *O. pedicellatum* Hincks, 1873, *O. pedunculatum* (Koch, 1876), *O. prenanti* Duboscq, 1925, *O. rosscoffensis* Batisse et Drajesco, 1967, *O. stellarum* Wailes, 1925, *O. trinacrium* Gruber, 1884, *O. ushakovi* Jankowski et Awerinczew, 1972.
2. *Corethria* Wright, 1861  
= *Vinarcon* Jankowski, 1981 syn. n.

*Corethria sertulariae* (Wright, 1858) (T.S., Fig. 22, I), *C. porcellanum* (Kent, 1881), *C. halacaridis* (Dons, 1942), *C. asteris* (Jankowski, 1981) comb. n. for *Vinarcon asteris* Jankowski, 1981.

3. *Shyzactinia* Jankowski, 1981  
*Shyzactinia multiramosa* (Wenzel, 1953) (T.S., Fig. 23, A).
4. *Spongiarcon* Jankowski, 1980  
*Spongiarcon variabilis* (Gruber, 1884) (T.S., Fig. 23, B).
5. *Loricodendron* Jankowski, 1973  
*Loricodendron hollandei* (Batisse, 1969) (T.S., Fig. 23, C).
6. *Crevicometes* Jankowski, 1981  
*Crevicometes murmanicus* Jankowski, 1981 (T.S., Fig. 23, E).

**FAMILY RHABDOPHRYIDAE JANKOWSKI, 1978**

Vermigemmin suctorians with unloricate, stalked, laterally flattened, ribbon-like or sac-like body. Rod-like tentacles are evenly distributed or placed on non-contractile actinophores of various shape.

- Habitat. Ectocommensals of marine crustaceans.
1. *Rhabdophrya* Chatton et Collin, 1910  
= *Stylarcon* Jankowski, 1981 syn. n.  
*Rhabdophrya trimorpha* Chatton et Collin, 1910 (T.S., Fig. 23, D), *R. nymphonis* (Gassovsky, 1916), *R. populiformis* (Gassovsky, 1916), *R. truncata* (Dons, 1915).
  2. *Hastarcon* Jankowski, 1981  
*Hastarcon islandicus* Jankowski, 1981 (T.S., Fig. 23, F).
  3. *Spinarcon* Jankowski, 1981  
*Spinarcon antennaris* Jankowski, 1981 (T.S., Fig. 23, G).
  4. *Trophogemma* Jankowski, 1970  
*Trophogemma poljanskyi* Jankowski, 1970 (T.S., Fig. 23, H).
  5. *Vostonica* Jankowski, 1994  
*Vostonica tenax* Jankowski, 1994 (T.S., Fig. 23, I).

**SUBCLASS ENDOGENIA COLLIN, 1912**

Suctorian ciliates with endogenous budding. Monogemmimic or polygemmic swimmers are produced internally. They are usually small, with encircling bands of cilia.

**ORDER ACINETIDA RAABE, 1964**

- = Acinetina Jankowski, 1978 syn. n.
- = Tokophryina Jankowski, 1978 syn. n.

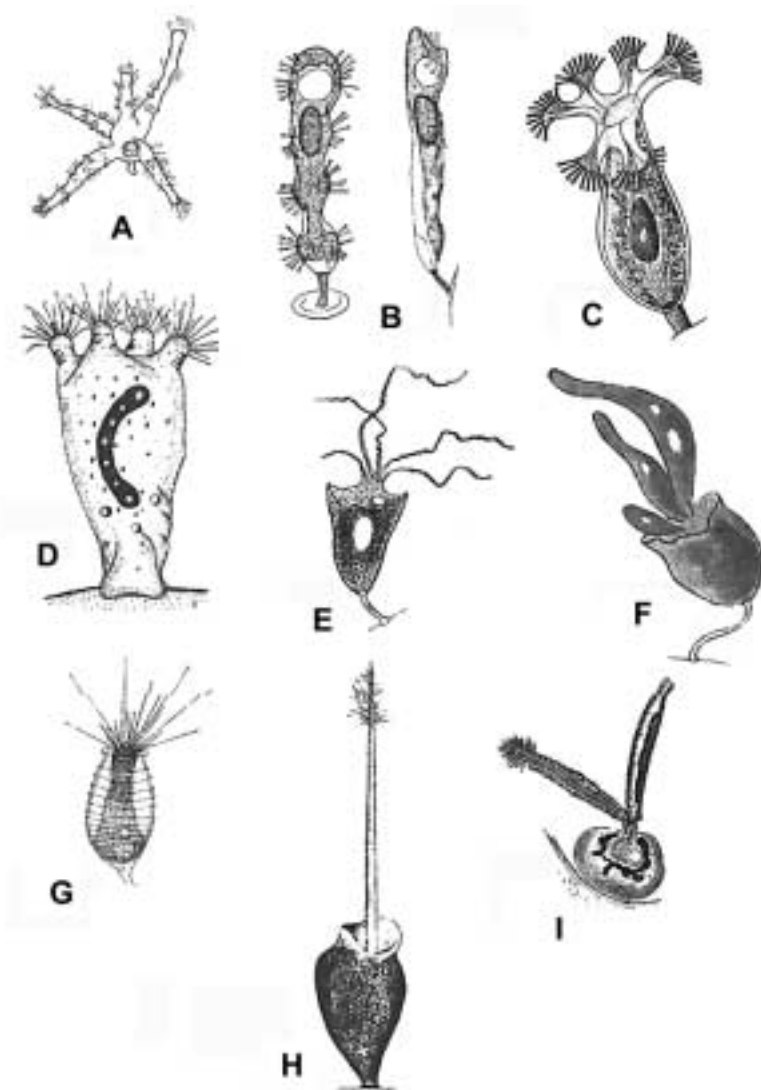


Fig. 22. Type species of the speleophryid and ophryodendrid suctorian genera. A – *Rondosomides lucicutiae* (Bowman, 1977), from Bowman, 1977; B – *Cucumophrya leptomesochrae* Kunz, 1936, from Kunz, 1936; C – *Asterifer faurei* (Guilcher, 1950), from Guilcher, 1950b; D – *Leboransia mysidacea* (Fernandez-Leborans et al., 1996), from Fernandez-Leborans et al., 1996; E – *Dentacineta campanuliformis* (Collin, 1912), from Collin, 1912; F – *Pleurophryodendron reversum* (Collin, 1909), budding, from Collin, 1912; G – *Thecacineta calix* (Schroder, 1901), from Matthes, 1956; H – *Ophryodendron abietinum* Claparede et Lachmann, 1859, from Claparede and Lachmann, 1859; I – *Corethria sertulariae* (Wright, 1858), budding, from Collin, 1912.

Suctorians with loricate and unloricate stalked adults. Capitulate tentacles in several fascicles or rows. The body usually flattened laterally.

**FAMILY ACINETIDAE EHRENBERG, 1838**

= Cryptophryidae Jankowski, 1978 syn. n.

Suctorians with a laterally flattened, trapezium-like, triangular or (rarely) disc-like body. Tentacles are arranged in two, rarely three fascicles or rows. As a rule actinophores are present. The macronucleus is ovoid or ribbon-like, never ramified. The presence of the stalk and all types of the lorica is characteristic of the family. Swimmers ovoid with longitudinal kineties.

Habitat. Commensals of marine and freshwater invertebrates and plants, as well as periphytic forms.

- 1. *Acineta* Ehrenberg, 1834<sup>5</sup>
- = *Plicophrya* Jankowski, 1975 syn. n.,
- = *Crossacineta* Jankowski, 1978 syn. n.
- = *Thalassacineta* Jankowski, 1981 syn. n.
- Acineta tuberosa* Ehrenberg, 1834 (T.S., Fig. 23, L),
- A. annulata* Wang et Nie Da Shu, 1932, *A. baikalica* (Swarzewsky, 1929), *A. benesaepa* Schulz, 1934, *A. branchicola* Precht, 1935, *A. brevicaulis* Rieder, 1936,

<sup>5</sup> In Zoological Record (1995, V. 131, P. 827 six new species from genus *Acineta* published by E. Dumas (1937) are given: *A. biligula* Dumas, 1937; *A. calculata* Dumas, 1937; *A. elaverina* Dumas, 1937; *A. mystacina* Dumas, 1937; *A. semiorbis* Dumas, 1937 and *A. tubicola* Dumas, 1937. Unfortunately, Dumas' work is not available to us. Therefore the species mentioned were omitted from the list.

*A. brevistyla* (Swarzewsky, 1929), *A. calkinsi* Curds, 1985, *A. calyx* Daday, 1907, *A. cattanei* Parona, 1883, *A. collini* Kahl, 1934, *A. commensalis* (Swarzewsky, 1929), *A. compressa* Claparede et Lachmann, 1859, *A. contorta* Gouurret et Roesel, 1886, *A. corophii* Collin, 1912, *A. corrugata* Stokes, 1894, *A. cothurnata* Claparede et Lachmann, 1859, *A. crassipes* Fric et Vavra, 1894, *A. crater* (Gajewskaja, 1933), *A. crustaceorum* Sand, 1899, *A. dentata* (Swarzewsky, 1929), *A. emaciata* Maupas, 1881, *A. euchaetae* Sewell, 1951, *A. flava* Stokes, *A. flexilis* Stokes, 1894, *A. fluviatilis* Stokes, 1885, *A. foetida* Maupas, 1881, *A. gammari* (Penard, 1920), *A. gelatinosa* Buck, 1884, *A. grahami* Allgen, 1955, *A. grandis* Kent, 1882, *A. harpacticola* Precht, 1935, *A. karamani* Hadzi, 1940, *A. laomedaeae* Precht, 1935, *A. lappacea* Stokes, 1885, *A. lasanicola* Maskell, 1887, *A. limnetis* Goodrich et Jahn, 1943, *A. maxima* Rieder, 1936, *A. minuta* Wailes, 1928, *A. nieuportensis* Sand, 1899, *A. nitocrae* Dovgal, 1984, *A. oceanica* Jankowski, 1981, *A. oequalis* Stokes, 1891, *A. operculariae* Engelmann, 1862, *A. ornata* Sand, 1899, *A. ovoidea* Allgen, 1951, *A. pachystylos* (Holm, 1925), *A. parroceli* Gouurret et Roesel, 1886, *A. poculum* Hertwig, 1875, *A. pulchra* Kahl, 1934, *A. puteana* Moniez, 1889, *A. pyriformis* (Stokes, 1891), *A. schulzi* Kahl, 1934, *A. simplex* Maskell, 1886, *A. socialis* Kent, 1869, *A. speciosa* Maskell, 1887, *A. sulcata* Dons, 1927, *A. symbiotica* Daday, 1907, *A. talitris* Jankowski, 1981, *A. tubulifera* (Swarzewsky, 1929), *A. variabilis* Nozawa, 1938, *A. zoothamnii* Hertwig, 1875.

2. *Trematosoma* Batisse, 1972

= *Conchacineta* Jankowski, 1978 syn. n.

= *Sparsacineta* Jankowski, 1978 syn. n.

= *Rimacineta* Jankowski, 1981 syn. n.

*Trematosoma boqueti* (Guilcher, 1950) (T.S., Fig. 23, K), *T. amphiasci* (Precht, 1935), *T. pusilla* (Maupas, 1881) comb. n. for *Acineta pusilla* Maupas, 1881, *T. complatana* (Gruber, 1884) comb. n. for *Acineta complatana* Gruber, 1884, *T. constricta* (Collin, 1909) comb. n. for *Acineta constricta* Collin, 1909, *T. falcata* (Jankowski, 1981) comb. n. for *Rimacineta falcata* Jankowski, 1981, *T. rotunda* (Allgen, 1952) comb. n. for *Acineta rotunda* Allgen, 1952.

3. *Acinetides* Swarzewsky, 1929

*Acinetides varians* Swarzewsky, 1929 (T.S., Fig. 23, J), *A. gruberi* Curds, 1985, *A. labiata* (Rieder, 1936), *A. triangularis* (Penard, 1920).

4. *Soracineta* Jankowski, 1978

*Soracineta dibdalteria* (Parona, 1881) (T.S., Fig. 24, A), *S. orchestii* Dovgal, 1999.

5. *Anthacineta* Jankowski, 1978

= *Noracineta* Jankowski, 1978 syn. n.

= *Semiacineta* Jankowski, 1978 syn. n.

*Anthacineta craterellus* (Collin, 1909) (T.S., Fig. 24,

B), *A. infundibuliformis* (Wang et Nie, 1933) comb. n. for *Acineta infundibuliformis* Wang et Nie, 1933, *Anthacineta swarzewskyi* (Collin, 1911) comb. n. for *Acineta swarzewskyi* Collin, 1911.

6. *Cryptacineta* Jankowski, 1978

*Cryptacineta operta* (Swarzewsky, 1929) (T.S., Fig. 24, C).

7. *Cryptophrya* Jankowski, 1973

*Cryptophrya obtecta* (Swarzewsky, 1929) (T.S., Fig. 24, E).

8. *Squalorophrya* Goodrich et Jahn, 1943

*Squalorophrya macrostyla* Goodrich et Jahn, 1943 (T.S., Fig. 27, G), *S. stenostyla* Hamilton et Jahn, 1947.

9. *Phyllacineta* Jankowski, 1978

*Phyllacineta jolyi* (Maupas, 1881) (T.S., Fig. 24, D), *P. tripharetrata* (Entz, 1902).

10. *Rondacineta* Jankowski, 1978

*Rondacineta muscicola* (Penard, 1914) (T.S., Fig. 24, F), *R. stellata* (Kent, 1881) comb. n. for *Acineta stellata* Kent, 1881.

11. *Slitarcon* Jankowski, 1986

*Slitarcon laevis* (Dons, 1918) (T.S., Fig. 24, G).

12. *Vasacineta* Jankowski, 1981

*Vasacineta cuspidata* (Kelllicott, 1885) (T.S., Fig. 24, H).

13. *Veracineta* Jankowski, 1978

*Veracineta tisbei* (Guilcher, 1950) (T.S., Fig. 24, J), *V. pyriformis* (Stokes, 1891).

**FAMILY ACINETOPSIDAE JANKOWSKI, 1978**

Acinetids with differentiation of tentacles into hypertrophic, agile prehensile and regular sucking ones. The body is trapezium-like, laterally flattened, loricate and stalked. The macronucleus is spherical or ovoid.

Habitat. Commensals of marine and freshwater invertebrates and plants.

1. *Acinetopsis* Robin, 1879

*Acinetopsis rara* Robin, 1879 (T.S., Fig. 24, I), *A. elegans* Swarzewsky, 1929, *A. tentaculata* Root, 1922.

**FAMILY TOKOPHRYIDAE JANKOWSKI, 1978**

Acinetid suctorians lacking lorica. The body ovoid, triangular or cylindrical, often flattened laterally. The macronucleus is spherical or ribbon-like. Capitulate tentacles are arranged in two or (rarely) more fascicles. Adhesion to substrate by stalk of different length.

Habitat. Commensals of marine and freshwater invertebrates and plants, as well as periphytic forms.

1. *Tokophrya* Bütschli, 1889

= *Trinacineta* Jankowski, 1981 syn. n.

= *Armiacineta* Jankowski, 1982 syn. n.

= *Sibiracineta* Jankowski, 1982 syn. n.

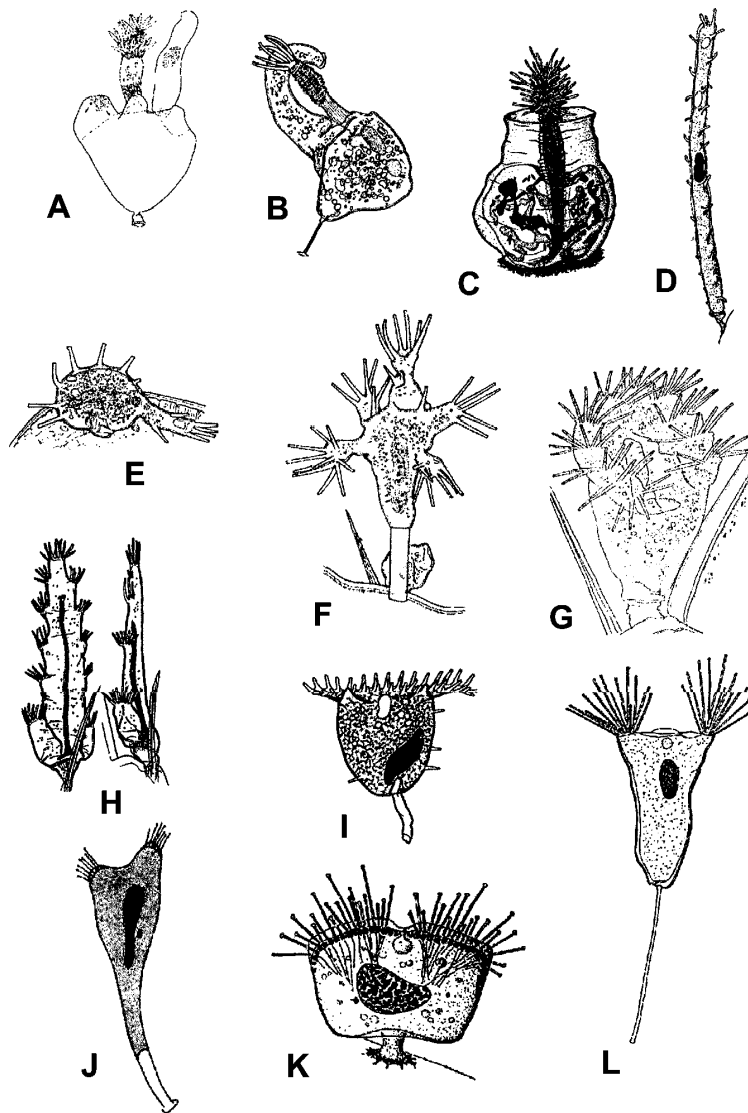


Fig. 23. Type species of the ophryodendrid and acinetid suctorian genera. A – *Shyzactinia multiramosa* (Wenzel, 1953), budding, from Wenzel, 1961; B – *Spongiarcon variabilis* (Gruber, 1884), from Jankowski, 1981; C – *Loricodendron hollandei* (Batisse, 1969), from Batisse, 1969; D – *Rhabdophrya trimorpha* Chatton et Collin, 1910, from Collin, 1912; E – *Crevicometes murmanicus* Jankowski, 1981, from Jankowski, 1981; F – *Hastarcon islandicus* Jankowski, 1981, from Jankowski, 1981; G – *Spinarcon antennaris* Jankowski, 1981, from Jankowski, 1981; H – *Tropogemma poljanskyi* Jankowski, 1970, from Jankowski, 1970; I – *Vostonica tenax* Jankowski, 1994, from Jankowski, 1994; J – *Acinetides varians* Swarczewsky, 1929, from Swarczewsky, 1929; K – *Trematosoma boqueti* (Guilcher, 1950), from Batisse, 1972; L – *Acineta tuberosa* Ehrenberg, 1834, orig.

= *Tokophryona* Jankowski, 1982 syn. n.  
 = *Basitokophrya* Jankowski, 1982 syn. n.

*Tokophrya quadripartita* (Claparede et Lachmann, 1859) (T.S., Fig. 25, A), *T. actinostyla* Collin, 1912, *T. beetoni* Small et Lynn, 1985, *T. bengalensis* Ghosh, 1929, *T. biloba* (Swarzewsky, 1929), *T. carchesii* (Claparede et Lachmann, 1859), *T. cordiformis* (Swarzewsky, 1929), *T. cornuta* (Swarzewsky, 1929), *T. crypturopi* (Swarzewsky, 1929), *T. cyclopum* (Claparede et Lachmann, 1859), *T. diaptomi* (Kellcott, 1885), *T. emarginata* Swarczewsky, 1929, *T. endemica* (Jankowski, 1982) comb. n. for *Sibiracineta endemica* Jankowski, 1982, *T. fasciculata* (Lopes-Ochoterena, 1964), *T. foecunda* (Swarzewsky, 1929), *T. globovata* (Bovee, 1981) comb. n. for *Testudinicola globovata* Bovee, 1981, *T. glomerata* Penard, 1920, *T. gracilipes* Penard, 1920, *T. grisca* Gajewskaja, 1933,

*T. infusionum* (Stein, 1859), *T. lemnarum* (Stein, 1859), *T. lobata* (Swarzewsky, 1929), *T. longicollis* Penard, 1920, *T. manuli* Matthes et Rebhan, 1983, *T. microcerberi* Delamare et Chappuis, 1956, *T. mollis* (Kent, 1882), *T. multifasciculata* Kormos, 1938, *T. niphargi* (Strouhal, 1939), *T. okobojiensis* (Goodich et Jahn, 1943), *T. ornata* Gajewskaja, 1933, *T. ovalis* (Swarzewsky, 1929), *T. parva* (Swarzewsky, 1929), *T. patagonica* (Collin, 1912), *T. pelagica* (Jankowski, 1982) comb. n. for *Tokophryona pelagica* Jankowski, 1982, *T. phreaticum* Ueno, 1962, *T. pulchra* (Swarzewsky, 1929), *T. pumila* (Swarzewsky, 1929), *T. pusilla* (Swarzewsky, 1929), *T. pyrum* (Claparede et Lachmann, 1859), *T. radiata* Gajewskaja, 1933, *T. seticola* (Jankowski, 1982) comb. n. for *Armiacineta seticola* Jankowski, 1982, *T. sphaerifera* (Swarzewsky, 1929), *T. steueri* Schroder, 1911, *T. tritoni* Guilcher,

1951, *T. troid* (Claparede et Lachmann, 1859), *T. vulgata* (Swarzewsky, 1929), *T. wenzeli* Matthes et Stiebler, 1970, *T. yastrebtsovi* Dovgal, 1993.

2. *Lecanodiscus* Jankowski, 1973

*Lecanodiscus longus* (Swarzewsky, 1928) (T.S., Fig. 25, C), *L. cyathos* (Swarzewsky, 1928), *L. robustus* (Swarzewsky, 1928).

3. *Listarcon* Jankowski, 1982

*Listarcon angarensis* Jankowski, 1982 (T.S., Fig. 25, D).

4. *Parastylophrya* Jankowski, 1978

*Parastylophrya tumida* (Gajewskaja, 1933) (T.S., Fig. 27, B).

5. *Muscophrya* Jankowski, 1978

*Muscophrya lycoperdon* (Penard, 1920) (T.S., Fig. 25, E).

6. *Pelagacineteta* Jankowski, 1978

= *Pseudocorynophrya* Small et Lynn, 1985 syn. n.  
*Pelagacineteta interrupta* (Schroder, 1901) (T.S., Fig. 25, F), *P. campanula* (Schroder, 1901), *P. multitentaculata* (Small et Lynn, 1985) comb. n. for *Pseudocorynophrya multitentaculata* Small et Lynn, 1985.

7. *Tokophryopsis* Swarzewsky, 1929

*Tokophryopsis gigantea* Swarzewsky, 1929 (T.S., Fig. 25, B).

8. *Talizona* Jankowski, 1981

*Talizona flexilis* (Kellcott, 1887) (T.S., Fig. 25, I).

#### FAMILY CORYNOPHRYIDAE JANKOWSKI, 1981

Suctorians with a massive spherical or cylindrical body and a well-developed stalk. Tentacles are regular capitate. They are agile, contractile and may be arranged in single apical fascicle or evenly distributed. The macronucleus is ribbon-like or ovoid.

Habitat. Commensals of marine invertebrates and algae.

1. *Corynophrya* Kahl, 1934

*Corynophrya lynghbyei* (Ehrenberg, 1834) (T.S., Fig. 25, G), *C. columbiae* (Wailes, 1943), *C. conipes* (Mereschkowsky, 1877), *C. francottei* (Sand, 1895), *C. macropus* (Meunier, 1910), *C. symbiotica* Jankowski, 1981.

2. *Andrusovia* gen. n.

*Andrusovia marina* (Andrusova, 1886) (T.S., Fig. 25, H) comb. n. for *Podophrya marina* Andrusova, 1886.

#### FAMILY CHOANOPHRYIDAE DOVGAL, FAM. N.

With the above diagnosis.

1. *Choanophrya* Hartog, 1901

*Choanophrya infundibulifera* (Hartog, 1881) (T.S., Fig. 25, L), *C. sessilis* Penard, 1920.

#### FAMILY DACTYLOSTOMATIDAE JANKOWSKI, 1978

Suctorian ciliates with bottle-like tentacles, arranged in two apical rows. The body sac-like, unflattened. The stalk is massive with apical widening (physon).

Habitat. Commensals of freshwater crustaceans from lake Baikal.

1. *Dactylostoma* Jankowski, 1967

*Dactylostoma collini* (Gajewskaja, 1929) (T.S., Fig. 26, A).

#### ORDER TRICHOPHRYIDA JANKOWSKI, 1978

= Marinectida Jankowski, 1981 syn. n.

= Pseudogemmida Jankowski, 1978 syn. n.

= Dendrosomatida Jankowski, 1978 syn. n.

= Dendrosomatina Jankowski, 1978 syn. n.

= Stylophryina Jankowski, 1978 syn. n.

Suctorians with a flattened stalkless body, with fascicles of capitate or rod-like tentacles on actinophores. The macronucleus is ovoid, ribbon-like or ramified. There are loricate forms, mainly with mucous lorica. Attachment to the substrate by the basal body surface, body protuberances or (in parasites) by tentacles.

#### FAMILY TRICHOPHRYIDAE BÜTSCHLI, 1879

= Marinectidae Jankowski, 1978 syn. n.

= Staurophryidae Jankowski, 1978 syn. n.

= Mucophryidae Jankowski, 1978 syn. n.

= Actinobranchiidae Jankowski, 1981 syn. n.

= Caprinianidae Jankowski, 1978 syn. n.

= Peltacinetidae Jankowski, 1981 syn. n.

Freshwater or marine suctorians attaching to the substrate by the basal surface of the body, its protuberances or specialized tentacles. The body unramified and unloricate or covered by mucous lorica. Tentacles are capitate or rod-like, arranged in fascicles or rows rarely on poorly developed actinophores.

Habitat. Commensals or parasites of water invertebrates and vertebrates as well as plankters.

1. *Trichophrya* Claparede et Lachmann, 1859<sup>6</sup>

<sup>6</sup> In Zoological Record (1995, V. 131, P. 827) four new species from genus *Trichophrya* are given with reference to E. Dumas' (1937) work: *T. fixa* Dumas, 1937; *T. limax* Dumas, 1937; *T. pistillaris* Dumas, 1937 and *T. viridis* Dumas, 1937. As noted above, Dumas' work (1937) is not available to us. Therefore the species mentioned were omitted from the list.

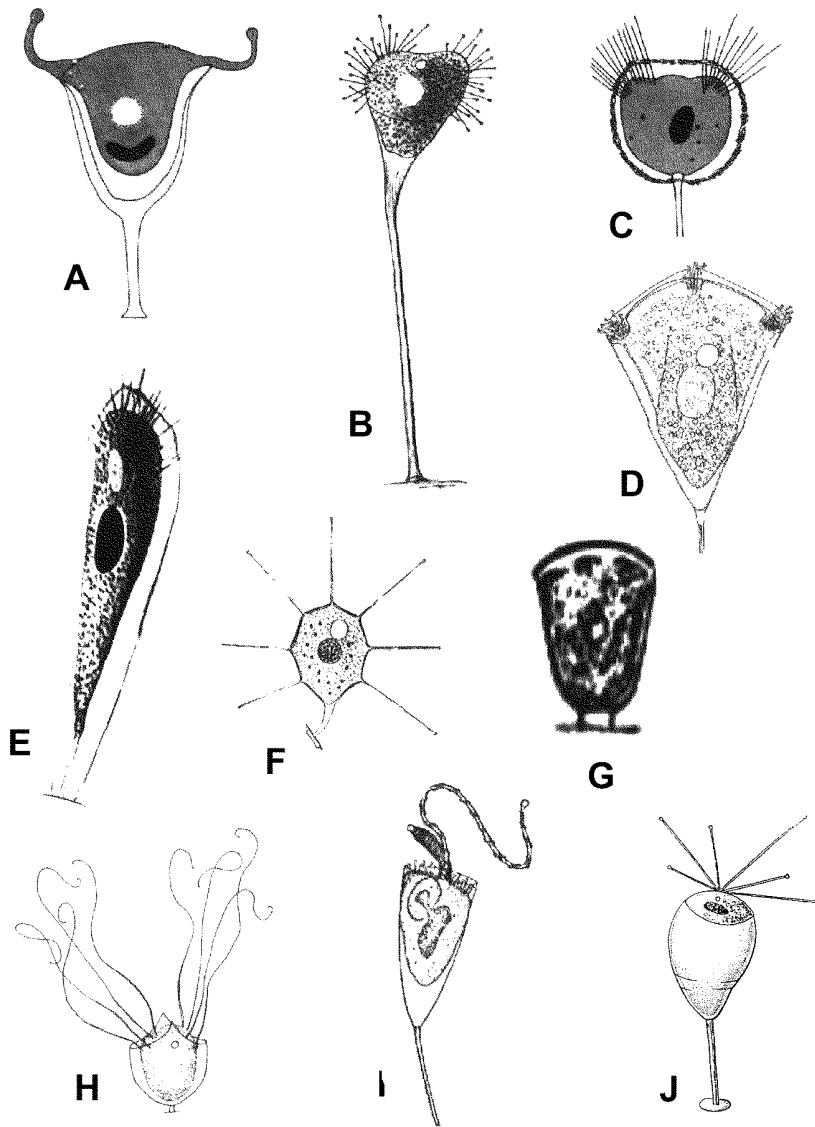


Fig. 24. Type species of the acinetid suctorian genera. A – *Soracineta dibdalteria* (Parona, 1881), from Curds, 1985a; B – *Anthacineta craterellus* (Collin, 1909), from Collin, 1912; C – *Cryptacineta operta* (Swarzewsky, 1929), from Swarczewsky, 1929; D – *Phyllacineta jolyi* (Maupas, 1881), from Jankowski, 1981; E – *Cryptophrya obtecta* (Swarzewsky, 1929), from Swarczewsky, 1929; F – *Rondacineta muscicola* (Penard, 1914), from Penard, 1914; G – *Slitarcon laevis* (Dons, 1918), from Kahl, 1934; H – *Vasacineta cuspidata* (Kellicott, 1885), from Kudo, 1946; I – *Acinetopsis rara* Robin, 1879, budding, from Kudo, 1946; J – *Veracineta tisbei* (Guilcher, 1950), from Guilcher, 1950b.

= *Gajewskajophrya* Matthes, 1988 syn. n.

= *Actinobranchium* Jankowski, 1967 syn. n.

*Trichophrya epistylidis* Claparede et Lachmann, 1859 (T.S., Fig. 26, B), *T. angulata* Dangeard, 1890, *T. brevis* (Goodrich et Jahn, 1943), *T. cambari* Small et Lynn, 1985, *T. mirabilis* Sand, 1899, *T. myriophylli* Penard, 1920, *T. odontophora* Sand, 1899, *T. ophrydii* Claparede et Lachmann, 1859, *T. pirosomae* Tregouboff, 1916, *T. salparum* Entz, 1884, *T. simplex* (Zacharias, 1893), *T. sinuosa* Stokes, 1886, *T. melosirae* (Gajewskaja, 1933) comb. n. for *Sphaerophrya melosirae* Gajewskaja, 1933.

2. *Brachyosoma* Batisse, 1975

*Brachyosoma brachypoda* (Stokes, 1885) (T.S., Fig. 26, C), *B. melo* (Penard, 1920), *B. bathynellae* (Chappuis, 1944), *B. oviformis* (Sand, 1899).

3. *Capriniana* Strand, 1928

*Capriniana piscium* (Bütschli, 1889) (T.S., Fig. 26, D), *C. variformis* (Li, 1985) comb. n. for *Trichophrya variformis* Li, 1985, *C. bivacuola* (Li, 1993) comb. n. for *Trichophrya bivacuola* Li, 1993.

4. *Staurophrya* Zacharias, 1893

*Staurophrya elegans* Zacharias, 1893 (T.S., Fig. 26, E).

5. *Tetraedrophrya* Zykoff, 1902

*Tetraedrophrya planktonica* Zykoff, 1902 (T.S., Fig. 26, F).

6. *Mucophrya* Gajewskaya, 1928

*Mucophrya pelagica* Gajewskaya, 1928 (T.S., Fig. 26, M).

7. *Marinecta* Jankowski, 1973

*Marinecta pelagica* (Daday, 1888) (T.S., Fig. 26, G), *M. columbiae* (Wailes, 1932), *M. danae* (Grontved, 1951), *M. massiliensis* (Gourret et Roeser, 1886).



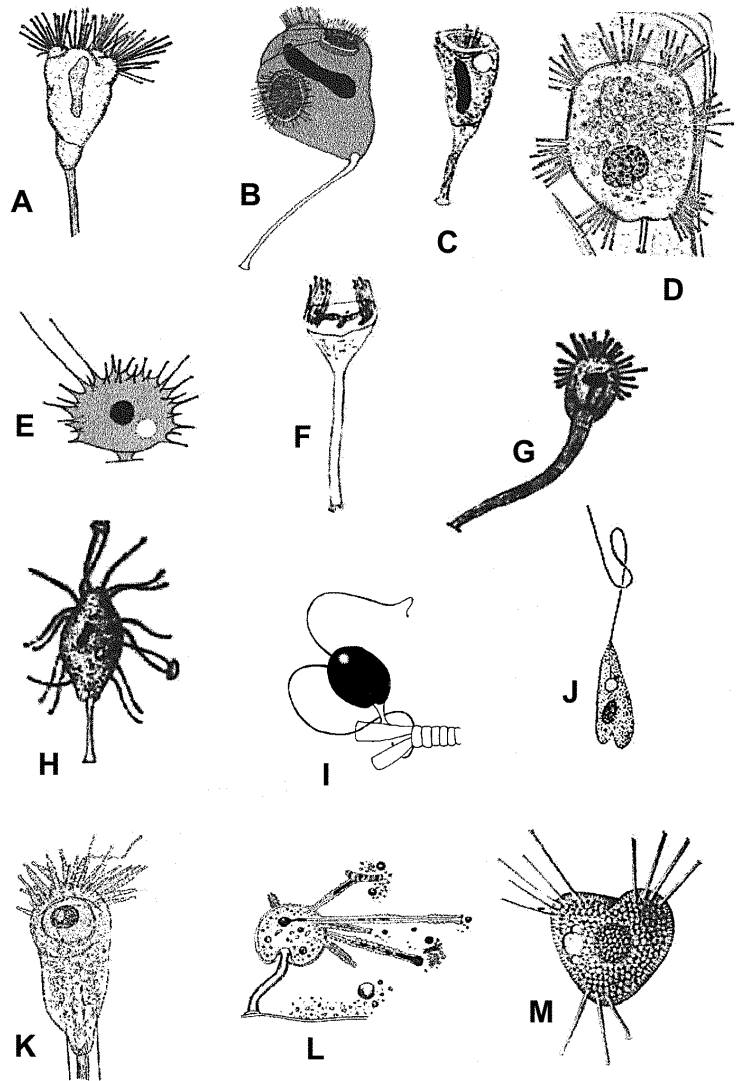


Fig. 25. Type species of the acinetid and trichophryid suctorian genera. A – *Tokophrya quadripartita* (Claparede et Lachmann, 1859), orig.; B – *Tokophryopsis gigantea* Swarczewsky, 1929, from Swarczewsky, 1929; C – *Lecanodiscus longus* (Swarczewsky, 1928), from Swarczewsky, 1928c; D – *Listarcon angarensis* Jankowski, 1982, from Jankowski, 1982; E – *Muscophrya lycoperdon* (Penard, 1920), from Curds, 1985c; F – *Pelagacineteta interrupta* (Schröder, 1901), from Kahl, 1934; G – *Corynophrya lyngbyei* (Ehrenberg, 1834), from Kahl, 1934; H – *Andrusovia marina* (Andrusova, 1886), from Kahl, 1934; I – *Talizona flexilis* (Kellicott, 1887), from Curds, 1985c; J – *Rhyncheta cyclopum* Zenker, 1886, from Kudo, 1946; K – *Riftus pygmaeus* (Swarczewsky, 1928), budding, from Jankowski, 1981; L – *Choanophrya infundibulifera* (Hartog, 1881), from Kudo, 1946; M – *Peltacineta cordiformis* (Schewiakoff, 1893), from Schewiakoff, 1893.

8. *Anarma* Goodrich et Jahn, 1943  
*Anarma multiruga* Goodrich et Jahn, 1943 (T.S., Fig. 26, H) (= *Testudinicola goodrichi* Bovee, 1981, syn. n.).  
 9. *Rhizobranchium* Jankowski, 1981  
*Rhizobranchium morchellii* (Tregouboff, 1916) (T.S., Fig. 26, I), *R. cionis* Jankowski, 1981.  
 10. *Peltacineta* Jankowski, 1981  
*Peltacineta cordiformis* (Schewiakoff, 1893) (T.S., Fig. 25, M).

**FAMILY RHYNCHETIDAE JANKOWSKI, 1978**

= Riftidae Jankowski, 1981 syn. n.

Suctorians parasitizing on freshwater crustaceans, attaching to the substrate by the basal body surface or protuberance. The key character of the family is the presence of several flexible, agile tentacles.

Habitat. Parasites of freshwater crustaceans.

1. *Rhyncheta* Zenker, 1866  
*Rhyncheta cyclopum* Zenker, 1866 (T.S., Fig. 25, J), *R. gammari* Eismond, 1890, *R. obconica* Hartog, 1901.  
 2. *Riftus* Jankowski, 1981  
*Riftus pygmaeus* (Swarczewsky, 1928) (T.S., Fig. 25, K).

**FAMILY DENDROSOMIDAE BÜTSCHLI, 1889**

= Stylophryidae Jankowski, 1978 syn. n.

Stalkless endogemmins with a ramified body. Tentacles are capitate, evenly distributed or arranged in fascicles on actinophores. Adhesion to the substrate by basal body surface or protuberance. The macronucleus is ramified or spherical.

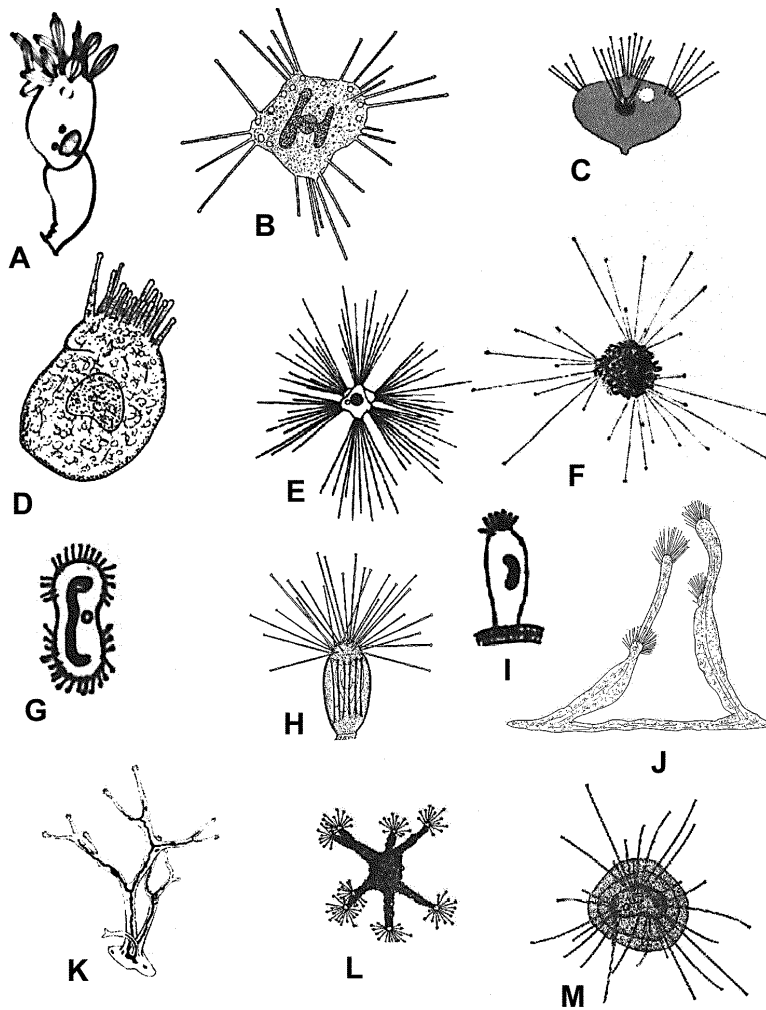


Fig. 26. Type species of the trichophryid and acinetid suctorian genera. A – *Dactylostoma collini* (Gajewskaja, 1929), from Gajewskaja, 1929; B – *Trichophrya epistylidis* Claparede et Lachmann, 1859, from Kudo, 1946; C – *Brachyosoma brachypoda* (Stokes, 1885), from Curds, 1985c; D – *Capriniana piscium* (Bütschli, 1889), orig.; E – *Staurophrya elegans* Zacharias, 1893, from Kudo, 1946; F – *Tetraedrophrya planktonica* Zykoff, 1902, from Zykoff, 1902; G – *Marinecta pelagica* (Daday, 1888), from Kahl, 1934; H – *Anarma multiruga* Goodrich et Jahn, 1943, from Goodrich et Jahn, 1943; I – *Rhizobranchium morchellii* (Tregouboff, 1916), from Kahl, 1934; J – *Dendrosoma radians* Ehrenberg, 1838, orig.; K – *Gorgonosoma arbuscula* Swarczewsky, 1928, from Swarczewsky, 1928a; L – *Astrophrya arenaria* Awerinzew, 1904, from Kudo, 1946; M – *Muco-phrya pelagica* Gajewskaja, 1928, from Gajewskaja, 1933.

Habitat. Freshwater or brackish-water periphytic and planktonic organisms as well as commensals of invertebrates.

1. *Dendrosoma* Ehrenberg, 1838  
= *Baikalophrya* Swarczewsky, 1928 syn. n.  
= *Baikalodendron* Swarczewsky, 1928 syn. n.,  
= *Lernaeophrya* Perez, 1903 syn. n.

*Dendrosoma radians* Ehrenberg, 1838 (T.S., Fig. 26, J) (= *Baikalophrya acanthogammari* Swarczewsky, 1928 syn. n., *B. digitata* Swarczewsky, 1928 syn. n., *B. lobata* Swarczewsky, 1928 syn. n., *Baikalodendron augustatum* Swarczewsky, 1928 syn. n.), *D. capitata* (Perez, 1903) comb. n. for *Lernaeophrya capitata* Perez, 1903.

2. *Gorgonosoma* Swarczewsky, 1928

*Gorgonosoma arbuscula* Swarczewsky, 1928 (T.S., Fig. 26, K).

3. *Astrophrya* Awerintzew, 1904

*Astrophrya arenaria* Awerinzew, 1904 (T.S., Fig. 26, L).

4. *Stylophrya* Swarczewsky, 1928

*Stylophrya polymorpha* Swarczewsky, 1928 (T.S., Fig. 27, A), *S. capitifera* Swarczewsky, 1928.

#### FAMILY ERASTOPHRYIDAE JANKOWSKI, 1978

Trichophryins attaching to the substrate (peritrichous ciliates) by characteristic organelles (cinctum or hemicinctum). Capitulate tentacles are evenly distributed on the body surface or arranged in fascicles on short actinophores. The macronucleus is ovoid or ribbon-like.

Habitat. Hypercommensals of freshwater fishes.

1. *Erastophrya* Faure-Fremiet, 1944

*Erastophrya chattoni* Faure-Fremiet, 1944 (T.S., Fig. 27, D).

2. *Chenophrya* Dovgal gen. n.

*Chenophrya wuchangensis* (Chen, 1964) (T.S., Fig. 27, E) comb. n. for *Erastophrya wuchangensis* Chen, 1964.

#### FAMILY SOLENOHRYIDAE JANKOWSKI, 1981

Stalkless, loricate suctorians attaching to the substrate by basal surface of the lorica. Tentacles are capitulate, the macronucleus is ovoid.

Habitat. Freshwater or brackish-water periphytic and planktonic organisms.

1. *Solenophrya* Claparede et Lachmann, 1859<sup>7</sup>

*Solenophrya crassa* Claparede et Lachmann, 1859 (T.S., Fig. 27, C), *S. bulbacea* Penard, 1920, *S. butschli* Sand, 1899, *S. calyciformis* Penard, 1920, *S. dubia* Penard, 1920, *S. flavescens* Penard, 1914, *S. inclusa* (Stokes, 1885), *S. massula* Penard, 1914, *S. odontophora* Stokes, 1887, *S. pera* (Stokes, 1885).

2. *Sphaeracineta* Jankowski, 1987

*Sphaeracineta estuarina* (Jones, 1973) (T.S., Fig. 27, F).

#### FAMILY PSEUDOGEEMMIDAE JANKOWSKI, 1978

Loricated suctorians with a single rod-like tentacle or several ones. Tentacles serve for both feeding and adhesion. The macronucleus is spherical or ellipsoid.

Habitat. Ectoparasites of freshwater or marine ciliates (suctorians and folliculins).

1. *Pseudogemma* Collin, 1912

*Pseudogemma pachystyla* Collin, 1912 (T.S., Fig. 27, H), *P. fraiponti* Collin, 1909, *P. keppeni* Collin, 1912, *P. metacinetarum* Nozawa, 1938.

2. *Pottsiocles* Corliss, 1960

*Pottsiocles infusoriorum* (Chatton et Lwoff, 1927) (T.S., Fig. 27, J).

#### ORDER ENDOSPHAERIIDA JANKOWSKI, 1978

Small ovoid forms with neither a stalk nor tentacles. Budding monogemmimic or polygemmic. Spherical or ellipsoid swimmers with several transversal kineties and perforatorium are characteristic of the order.

#### FAMILY ENDOSPHAERIIDAE JANKOWSKI, 1978

With characteristics of the order.

Habitat. Freshwater and marine intracellular or tissue parasites of ciliates, turbellarians and bivalve molluscs.

1. *Endosphaera* Engelmann, 1876

*Endosphaera engelmanni* Entz, 1896 (T.S., Fig. 27, K), *E. elisabetharum* Guhl, 1985, *E. terebrans* Matthes et Guhl, 1973.

2. *Parendosphaera* Jankowski, 1981

*Parendosphaera multifilis* (Gonnert, 1935) (T.S., Fig. 27, I).

3. *Acoelophthirius* Jankowski, 1981

*Acoelophthirius acronifer* Jankowski, 1981 (T.S., Fig. 27, L), *A. doerjesi* Jankowski, 1981.

#### SUBCLASS EVAGINOGENIA JANKOWSKI, 1978

Suctorians with evaginative budding (inver-sogemmy).

#### ORDER DISCOPHRYIDA JANKOWSKI, 1975

= Discophryina Jankowski, 1981 syn. n.

= Heliophryida Jankowski, 1981 syn. n.

Predominantly stalked forms or forms attaching to the substrate by an adhesive structure (disc) which is a modified stalk. Several forms are attached by protuberance of body or stylotheca. The body is disc-like, rarely spheroid or cylindrical in shape. There are both forms lifted over the substrate and spread forms. Tentacles are capitate. As a rule, actinophores are absent. Polymerisation of contractile vacuoles (up to several tens) is also characteristic of the representatives of the order.

#### FAMILY DISCOPHRYIDAE COLLIN, 1912

= Coronodiscophryidae Jankowski, 1981 syn. n.

= Cyathodiscophryidae Jankowski, 1981 syn. n.

= Multifasciculatidae Jankowski, 1981 syn. n.

Unloricate, stalked suctorians with a flattened disc-like, rarely sac-like body. Tentacles are capitate, arranged in fascicles or distributed along the body. The macronucleus is ovoid, ribbon-like or ramified.

Habitat. Mainly ectocommensals of imago of water insects and adults of crustaceans, also freshwater periphytonic forms.

1 *Discophrya* Lachmann, 1859

= *Venodiscophrya* Jankowski, 1981 syn. n.

= *Ferodiscophrya* Jankowski, 1981 syn. n.

= *Coronodiscophrya* Jankowski, 1981 syn. n.

= *Epidiscophrya* Jankowski, 1981 syn. n.

= *Paradiscophrya* Jankowski, 1981 syn. n.

= *Cyathodiscophrya* Jankowski, 1981 syn. n.

*Discophrya ferrumequinum* (Ehrenberg, 1840) (T.S., Fig. 28, B), *D. astaci* (Claparede et Lachmann, 1859),

*D. brachystyla* Kormos, 1938, *D. coperniciana* Wietrzy-

kowski, 1914, *D. cothurnata* (Weisse, 1848), *D.*

*cyathostyla* Matthes, 1954, *D. cylindrica* (Perty, 1852),

*D. diademiformis* (Pritchard, 1861) comb. n. for *Acineta*

*diademiformis* Pritchard, 1861, *D. elegans* (Goodrich

<sup>7</sup> In Zoological Record (1995, V. 131, P. 827) the new species *Solenophrya crumilla* Dumas, 1937 is given. As noted above, Dumas' work (1937) work is not available to us. Therefore the species mentioned were omitted from the list.

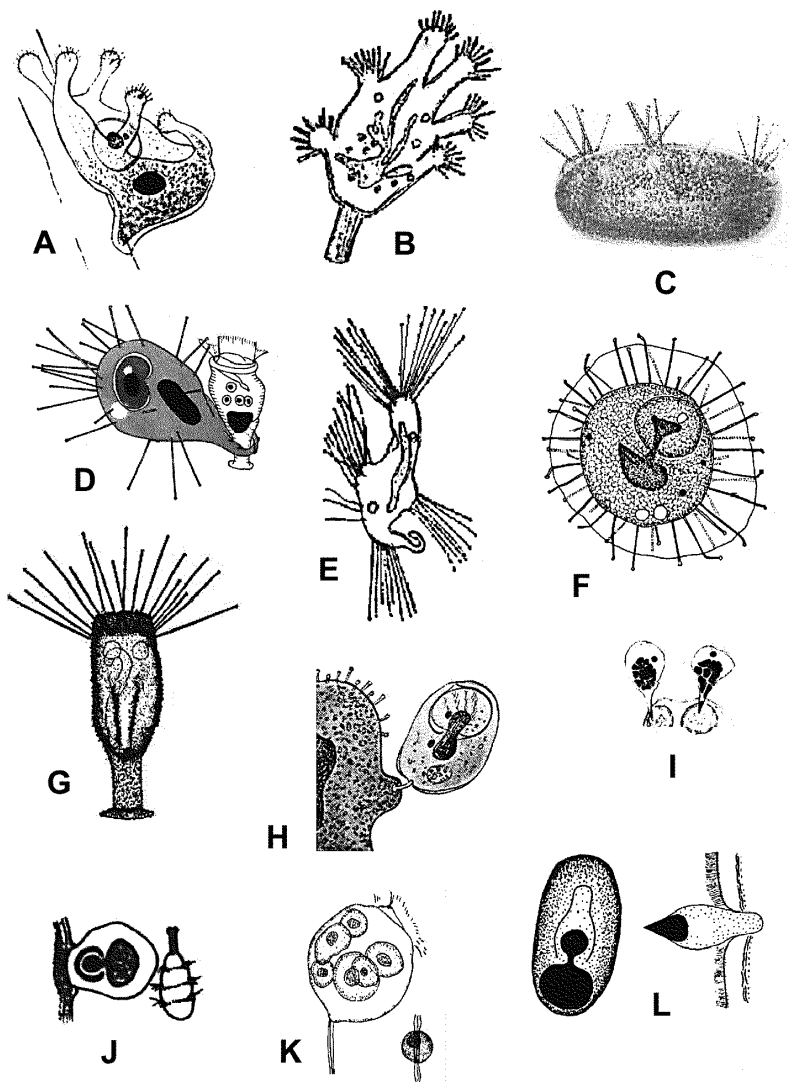


Fig. 27. Type species of the trichophryid, endosphaeriid and acinetid suctorian genera. A – *Stylophrya polymorpha* Swarczewsky, 1928, from Swarczewsky, 1928a; B – *Parastyllophrya tumida* (Gajewskaja, 1933), from Gajewskaja, 1933; C – *Solenophrya crassa* Claparede et Lachmann, 1859, from Claparede and Lachmann, 1859; D – *Erastophrya chattoni* Faure-Fremiet, 1944, budding specimen on the peritrichous host, from Curds, 1985c; E – *Chenophrya wuchangensis* (Chen, 1964), from Matthes et al., 1988; F – *Sphaeracineteta estuarina* (Jones, 1973), budding, from Jones, 1973; G – *Squalorophrya macrostyla* Goodrich et Jahn, 1943, from Goodrich and Jahn, 1943; H – *Pseudogemma pachystyla* Collin, 1912, budding, from Collin, 1912; I – *Parendosphaera multifilis* (Gonnert, 1935), budding, from Gonnert, 1935; J – *Pottsioctes infusoriorum* (Chatton et Lwoff, 1927), budding trophont and swarmer, from Kahl, 1934; K – *Endosphaera engelmanni* Entz, 1896, six specimens within the host cell, orig. and swarmer, from Kudo, 1946; L – *Acoelophthirus doerjesi* Jankowski, 1981, from Dorjes, 1979.

et Jahn, 1943), *D. elongata* (Claparede et Lachmann, 1859), *D. gessneri* Matthes, 1954, *D. grassa* Gajewskaja, 1932, *D. helmidis* Matthes, 1954, *D. helophori* Matthes et Plachter, 1975, *D. hydrochi* Matthes, 1953, *D. inclinata* (Kellicott, 1887), *D. kormosi* Matthes, 1954, *D. laccobii* Matthes, 1954, *D. lata* Rieder, 1936, *D. lemnae* (Mereschkowsky, 1878) comb. n. for *Podophrya lemnae* Mereschkowsky, 1878, *D. lichtensteinii* (Claparede et Lachmann, 1859), *D. minuta* Nozawa, 1938, *D. ochthebii* Matthes, 1954, *D. prismatica* Holm, 1925, *D. scyphostyla* (Collin, 1912), *D. spatulata* Rieder, 1936, *D. tumida* Gajewskaja, 1933, *D. wrzesniowski* (Kent, 1882).

2. *Setodiscophrya* Jankowski, 1981

= *Mesodiscophrya* Jankowski, 1981 syn. n.

*Setodiscophrya hydroi* (Matthes, 1954) (T.S., Fig. 28, C), *S. erlangensis* (Matthes, 1954), *S. deplanata* (Matthes, 1954), *S. operculariae* (Stein, 1859) comb.

n. for *Podophrya operculariae* Stein, 1859, *S. setarcon* (Jankowski, 1981) comb. n. for *Mesodiscophrya setarcon* Jankowski, 1981, *S. steinii* (Claparede et Lachmann, 1859) comb. n. for *Podophrya steinii* Claparede et Lachmann, 1859, *S. robusta* Nozawa, 1938 comb. n. for *Discophrya robusta* Nozawa, 1938.

3. *Misacineta* Jankowski, 1978

*Misacineta cybistri* (Collin, 1912) (T.S., Fig. 28, D), *M. acilii* (Collin, 1912).

#### FAMILY PRODISCOPHYRIDAE JANKOWSKI, 1978

Discophryid suctorians with a stalked spheroid body. Capitulate tentacles are evenly distributed over the body surface. The macronucleus is spherical. The key characteristic of the family is anisogamic conjugation involving ciliary microconjugant similar to the swarmer.

Habitat. Freshwater periphytonic forms.

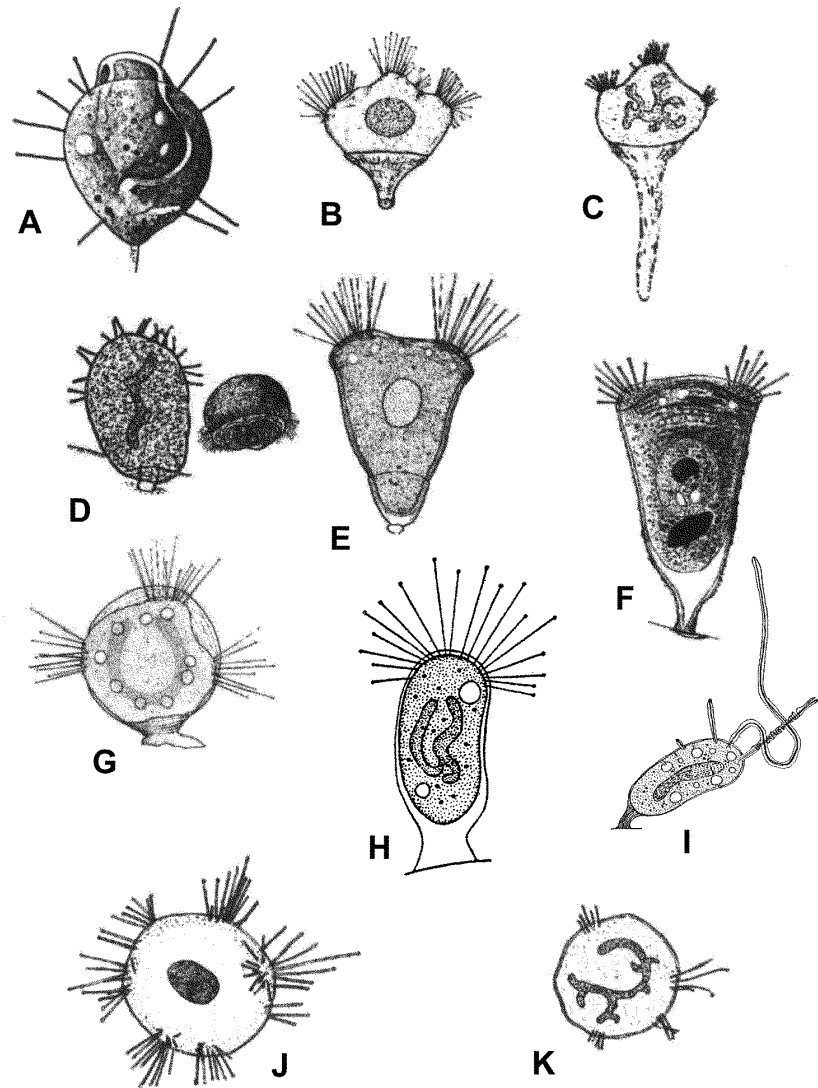


Fig. 28. Type species of the discophryid suctorian genera. A – *Prodiscophrya solaris* (Stein, 1859), budding, from Guilcher, 1951; B – *Discophrya ferrumequinum* (Ehrenberg, 1840), orig.; C – *Setodiscophrya hydroi* (Matthes, 1954), from Matthes, 1954e; D – *Misacineta cybistri* (Collin, 1912), trophont and swarmer, from Collin, 1912; E – *Periacineta buckei* (Kent, 1882), from Matthes, 1954e; F – *Kormosia linguifera* (Claparede et Lachmann, 1859), from Collin, 1912; G – *Elatodiscophrya stammeri* (Matthes, 1954), from Matthes, 1974; H – *Peridiscophrya japonica* Nozawa, 1938, from Nozawa, 1938; I – *Rhynchophrya palpans* Collin, 1909, from Collin, 1912; J – *Heliodiscophrya rotunda* (Hentschel, 1916), orig.; K – *Cyclophrya magna* Gonnert, 1935, orig.

1. *Prodiscophrya* Kormos, 1935

*Prodiscophrya solaris* (Stein, 1859) (T.S., Fig. 28, A), *P. endogama* J. Kormos et K. Kormos, 1956.

**FAMILY PERIACINETIDAE JANKOWSKI, 1978**

- = Caracatharinidae Jankowski, 1981 syn. n.
- = Catharinidae Jankowski, 1981 syn. n.

Discophryins with tectinous lorica or stylothea, laterally flattened or (rarely) sac-like body and clavate tentacles arranged in fascicles. The macronucleus is ellipsoid, ribbon-like or ramified.

Habitat. Commensals of freshwater invertebrates and periphytonic forms.

1. *Periacineta* Collin, 1909

- = *Anisarcon* Jankowski, 1981 syn. n.
- = *Arcodiscophrya* Jankowski, 1981 syn. n.
- = *Tomodiscophrya* Jankowski, 1981 syn. n.
- Periacineta buckei* (Kent, 1882) (T.S., Fig. 28, E),

*P. gyrini* Dovgal, 1993, *P. heraldica* (Jankowski, 1981) comb. n. for *Arcodiscophrya heraldica* Jankowski, 1981, *P. hydrochi* (Matthes, 1954) comb. n. for *Discophrya hydrochi* Matthes, 1954, *P. koeppli* (Matthes, 1954), *P. laccophili* (Matthes, 1954), *P. molesta* (Matthes, 1954), *P. notonectae* (Claparede et Lachmann, 1859), *P. paratuberosa* (Nie et Ho, 1943) comb. n. for *Acineta paratuberosa* Nie et Ho, 1943, *P. periacinetoides* (Nozawa, 1938), *P. striata* Dovgal, 1993, *P. urceolata* (Stokes, 1885).

2. *Kormosia* Dovgal gen. n.

*Kormosia linguifera* (Claparede et Lachmann, 1859) (T.S., Fig. 28, F) comb. n. for *Acineta linguifera* Claparede et Lachmann, 1859.

3. *Elatodiscophrya* Jankowski, 1978

*Elatodiscophrya stammeri* (Matthes, 1954) (T.S., Fig. 28, G), *E. hochi* (Matthes, 1954).

4. *Peridiscophrya* Nozawa, 1938 (non Kormos, 1938)

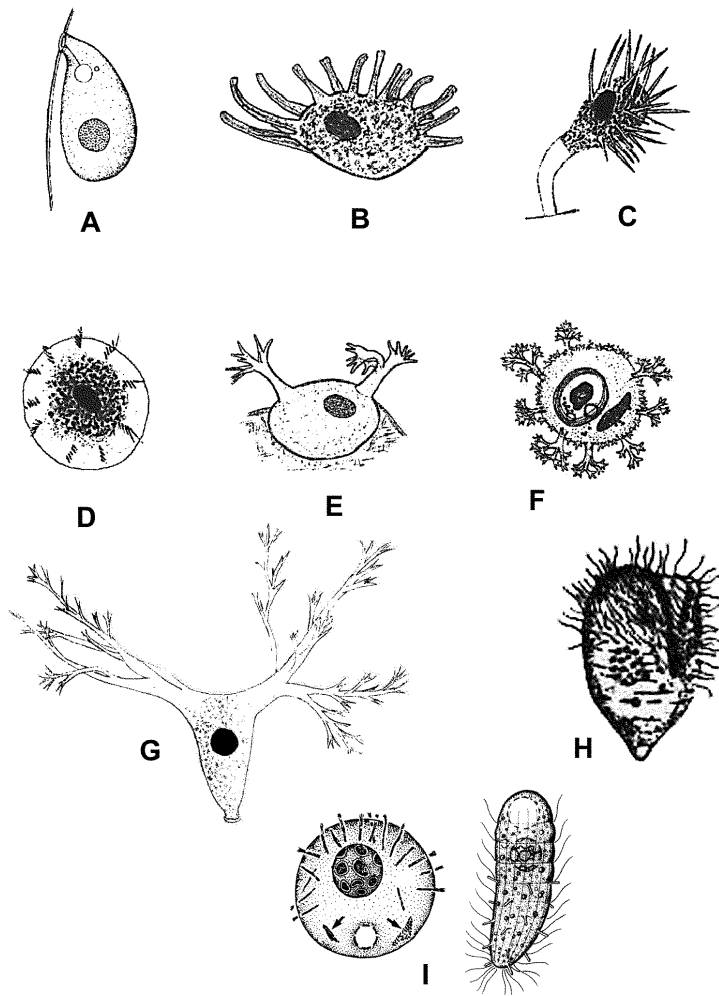


Fig. 29. Type species of the tripanococcid, dendrocometid and cyathodiniid suctorian genera. A – *Tripanococcus rotiferorum* Stein, 1867, from Matthes, 1971; B – *Stylocometes digitatus* (Claparede et Lachmann, 1859), orig.; C – *Echinophrya horrida* Swarczewsky, 1928, from Swarczewsky, 1928c; D – *Discosomatella tenella* (Swarzewsky, 1928), from Swarczewsky, 1928b; E – *Dendrocometes paradoxus* Stein, 1851, orig.; F – *Niscometes peregrinus* (Small et Lynn, 1985), budding, from Small and Lynn, 1985; G – *Cometodendron erectum* Swarczewsky, 1928, from Swarczewsky, 1928b; H – *Cyathodinium conicum* Cunha, 1914, from Kudo, 1946; I – *Enchelyomorpha vermicularis* (Smith, 1899), trophont and swarmer, from Foissner and Foissner, 1995.

= *Catharina* Kormos, 1957 syn. n.  
= *Caracatharina* Kormos, 1968 syn. n.

*Peridiscophrya japonica* Nozawa, 1938 (T.S., Fig. 28, H), *P. florea* (Kormos, 1957) comb. n. for *Catharina florea* Kormos, 1957, *P. crassipes* (Rieder, 1936) comb. n. for *Paracineta crassipes* Rieder, 1936.

#### FAMILY RHYNCHOPHRYIDAE JANKOWSKI, 1978

Stalked, unloricate suctorians with laterally flattened, elongated body and several contractile, agile tentacles. The macronucleus is ribbon-like.

Habitat. Ectoparasites of discophryin suctorians.

1. *Rhynchophrya* Collin, 1909

*Rhynchophrya palpans* Collin, 1909 (T.S., Fig. 28, I).

#### FAMILY HELIOPHRYIDAE CORLISS, 1979

Evaginogemmins with discoid and often small body flattened on the substrate. There is no stalk or lorica but tectinous adhesive disc is present. Tentacles

are knobbed and extensible, solitary or arranged in several fascicles. The macronucleus is ovoid or ramified.

Habitat. Freshwater periphytonic forms and commensals of invertebrates.

1. *Heliophrya* De Saedeleer et Tellier, 1930

= *Paraheliophrya* Jankowski, 1978 syn. n.

*Heliophrya rotunda* (Hentschel, 1916) (T.S., Fig. 28, J), *H. minima* (Rieder, 1936), *H. sinuosa* (Rieder, 1936).

2. *Cyclophrya* Gonnert, 1935

*Cyclophrya magna* Gonnert, 1935 (T.S., Fig. 28, K), *C. katharinae* Kormos, 1960.

#### ORDER TRIPANOCOCCINA DOVGAL, ORD. N.

With the above diagnosis.

#### FAMILY TRIPANOCOCCIDAE DOVGAL, FAM. N.

With characteristics of the order.

1. *Tripanococcus* Stein, 1867

*Tripanococcus rotiferrorum* Stein, 1867 (T.S., Fig. 29, A).

**ORDER DENDROCOMETIDA RAABE, 1964**

Inversogemmins with a hemispherical, disc-like, vase-like or spindle-shaped body. The presence of ramified or rod-like tentacles is characteristic.

**SUBORDER STYLOCOMETINA JANKOWSKI, 1981**

Stalked or stalkless suctorian ciliates with ovoid, sac-like or disc-like body. The rod-like, unramified tentacles are randomly distributed or arranged into rows.

**FAMILY STYLOCOMETIDAE JANKOWSKI, 1981**

= Discosomatellidae Jankowski, 1978 syn. n.

Unstalked and stalked suctorians with ovoid, sac-like or disc-like body spread over the substrate. Tentacles are rod-like with a well-developed axonema, evenly distributed or arranged in rows.

Habitat. Ectocommensals of freshwater isopod and amphipod crustaceans.

1. *Stylocometes* Stein, 1876

*Stylocometes digitatus* (Claparede et Lachmann, 1859) (T.S., Fig. 29, B).

2. *Discosomatella* Corliss, 1960

*Discosomatella tenella* (Swarzewsky, 1928) (T.S., Fig. 29, D).

3. *Echinophrya* Swarczewsky, 1928

*Echinophrya horrida* Swarczewsky, 1928 (T.S., Fig. 29, C), *E. stenaselli* (Matjasic, 1963) comb. n. for *Choanophrya stenaselli* Matjasic, 1963.

**FAMILY ENCHELYOMORPHIDAE AUGUSTIN ET FOISSNER, 1992**

Stalkless suctorians with spherical trophonts possessing rod-like tentacles randomly positioned on the one of the body sides. The macronucleus is spheroid. Invaginative budding with synchronous formation of two protomits is characteristic. The swarmer is spindle-shaped with numerous transversal kineties and several rod-like tentacles at the posterior end. The mitochondria are lacking but hydrogenosomes and autophagous vacuoles are present.

Habitat. Anaerobic plankters, inhabitants of the activated sludge (Ettl, 2001) and soil (Foissner, 1998).

1. *Enchelyomorpha* Kahl, 1930

*Enchelyomorpha vermicularis* (Smith, 1899) (T.S., Fig. 29, I).

**SUBORDER DENDROCOMETINA DOVGAL, SUBORD. N.**

With the above diagnosis.

**FAMILY DENDROCOMETIDAE STEIN, 1851**

Hemispherical or disc-like, spread forms with ramified tentacles. The macronucleus is spherical or ovoid.

Habitat. Ectocommensals of freshwater gammarid crustaceans.

1. *Dendrocometes* Stein, 1851

= *Dendrocometides* Swarczewsky, 1928 syn. n.

*Dendrocometes paradoxus* Stein, 1851 (T.S., Fig. 29, E and Fig. 2), *D. densus* Swarczewsky, 1928, *D. discoideus* Swarczewsky, 1928, *D. gigas* Swarczewsky, 1928, *D. gracilis* Swarczewsky, 1928, *D. robustrus* Swarczewsky, 1928, *D. priscus* (Swarzewsky, 1928) comb. n. for *Dendrocometides priscus* Swarczewsky, 1928.

2. *Niscometes* Jankowski, 1987

*Niscometes peregrinus* (Small et Lynn, 1985) (T.S., Fig. 29, F).

**FAMILY COMETODENDRIDAE JANKOWSKI, 1978**

Suctorians with a vase-like branched body lifted over the substrate and ramified tentacles. The macronucleus is spherical. The body attaches to the substrate by its basal protuberance.

Habitat. Commensals of freshwater gammarid crustaceans attaching to the leg setae.

1. *Cometodendron* Swarczewsky, 1928

*Cometodendron erectum* Swarczewsky, 1928 (T.S., Fig. 29, G), *C. brevimantum* Swarczewsky, 1928, *C. clavatum* Swarczewsky, 1928, *C. digitatum* Swarczewsky, 1928, *C. longimantum* Swarczewsky, 1928, *C. palmetta* Swarczewsky, 1928, *C. palmettoideum* Swarczewsky, 1928, *C. pedunculatum* Swarczewsky, 1928, *C. raphanus* Swarczewsky, 1928, *C. rhabdophryoideum* Swarczewsky, 1928, *C. subtile* Swarczewsky, 1928, *C. spissum* Swarczewsky, 1928,

**ORDER CYATHODINIIDA JANKOWSKI, 1975**

Suctorians with a pyriform body, retaining ciliature at the trophont stage. Very short tentacles (endospirts) are arranged in rows. Budding with production of two ciliated protomits simultaneously.

**FAMILY CYATHODINIIDAE DA CUNHA, 1914**

With characteristics of the order.

Habitat. Endocommensals of digestive tract of guinea pigs.

1. *Cyathodinium* da Cunha, 1914

*Cyathodinium conicum* Cunha, 1914 (T.S., Fig. 29, H), *C. breve* Cunha et Freitas, 1940, *C. chagasi* Cunha et Freitas, 1936, *C. cunhai* Nie, 1950, *C. indiae* Bhaskar Rao, 1976, *C. intermedius* Cunha et Freitas, 1940, *C. parvus* Cunha et Freitas, 1940, *C. pentagonum* Cunha et Freitas, 1940, *C. scotti* Cunha et Freitas, 1940, *C. sphaericum* Kopperi, 1935, *C. vesiculosum* Cunha, 1914.

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*The manuscript is presented by A.A. Dobrovolskij*

An International Journal "Protistology" accepts original, substantial and critical manuscripts in any area of investigation of protists. Suitable topics include: morphology, taxonomy, systematics, phylogeny, ecology, behaviour, physiology, biochemistry, genetics, cell and molecular biology of protozoa, algae and zoosporic fungi.

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The size of manuscript is not limited in general. It is recommended to follow the usual structure of the paper arranged as follows: Title page (Full title of article, Name(s) of author(s), Addresses, Summary (summary should be a single paragraph not more than half page, and Key words), Text (Introduction, Material and Methods, Results, Discussion, Acknowledgements, References, Address for correspondence with e-mail), Tables and Legends to the Figures. The preferable position of tables and figures in the text should be indicated on the margins of the printed version of the manuscript. The names of species and genera must be italicized.

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Figure legends on separate sheets should be brief and precise. They must not repeat, expand or specify the information in the text. Legends to separate figures should contain the title of the figure and the explanation of symbols used in the figure (letter symbols are given alphabetically, then follows the explanation of graphic symbols):

Fig. 1. Floating form of *Korotnevella discophora*.  
*n* – nucleus, *p* – pseudopodia.

Legends to plates should have the general title of the plate, the titles of separate positions and explanation of symbols:

Fig. 5. Microsporidia from the gut of *Gryllus bimaculatus*. *A* – epithelium of the gut with invaded enterocytes; *B* – parasitophorous vacuole with dividing meront; *C* – early stages of sporogenesis, *D* – mature spore. Abbreviations: *b* – basal plate of epithelium, *e* – exospore, *fv* – food vacuole, *pv* – parasitophorous vacuole; *arrow* – a fragment of everted polar filament.

One and the same letter symbol should mark one and the same structure throughout the figures. If letter symbols are repeated, the explanation is given only the first time the symbol is used. In the following figure legends it should be written: for explanation of other symbols see Fig. 2.

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- Karpov S.A. 1982. The ultrathin structure of choanoflagellate *Monosiga ovata*. Tsitologiya. 24, 4, 400-404 (in Russian with English summary).  
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