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IRKANA GEN. NOV. (CILIOPHORA, SUCTOREA), A SYMBIONT OF THE COLONIAL PERITRICH *CARCHESIUM* IN LAKE BAIKAL

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ABSTRACT

Elodea canadensis near a wharf in Listvenka bears colonies of *Carchesium* richly infested with a new species of small suctorians, supposedly modified tokophryids. The description of this suctorian is illustrated with a series of drawings made with the aid of an ocular reticle and thus retaining the exact proportions of the cells, of their tentacles and host stalks; this series shows growth stages and individual variations in cell size, shape, number and distribution of tentacles. Cells are bag-like, with a somewhat erratic distribution of retractile acrotenic tentacles in 2–3, rarely 4 indistinct groups on the cell surface, without actinophores, with an ovoid macronucleus and homogenous attachment disc (fixon), without a stalk; reproduction is by internal budding. New combination: *Tetrahymena hydrae* (Entz, 1912) Jankowski comb. n. for *Balantidium hydrae* Entz, 1912 (endoparasite of co-existing *Hydra baicalensis*).

Key words: *Carchesium*, *Irkana*, Peritrichia, Suctorea, symbiosis

IRKANA GEN. NOV. (CILIOPHORA, SUCTOREA), СИМБИОНТ КОЛОНИАЛЬНОЙ ПЕРИТРИХИ *CARCHESIUM* В ОЗЕРЕ БАЙКАЛ

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РЕЗЮМЕ

На элодее (*Elodea canadensis*) у причала Листвянки колонии *Carchesium* в изобилии заселены новым видом мелких сукторий, вероятно видоизмененными токофриидами. Эта суктория показана на серии рисунков, выполненных с помощью окулярной сетки, с точными пропорциями клеток, их щупалец и стебельков хозяина; зарисованы стадии роста и индивидуальные вариации размеров, формы клеток, числа и положения щупалец. Клетки мешковидные, с почти беспорядочным положением сократимых акротенных щупалец в 2–3, реже в 4 нечетких пучках, без актинофоров, с овальным макронуклеусом и гомогенным прикрепительным диском (фиксоном), без стебелька; размножение внутренним почкованием. Новая комбинация: *Tetrahymena hydrae* (Entz, 1912) Jankowski comb. n. для *Balantidium hydrae* Entz, 1912 (эндопаразит в *Hydra baicalensis* в том же биотопе).

Ключевые слова: *Carchesium*, *Irkana*, Peritrichia, Suctorea, симбиоз

INTRODUCTION

Many species of suctorians are associated with other ciliates as commensals and parasites in fresh waters and seas of the world; there are also obligate symbionts of pelagic diatoms and cyanobacteria. Rhynchodids *Hypocoma*, supposed predecessors of Suctorea, are also obligate parasites of protists. In freshwater, the most common symbionts (in the widest sense of this term, as accepted now – both commensals and parasites) are *Tokophrya*, *Tokophryella*, *Urnula*, *Endosphaera*, *Erastophrya*, *Mistarcon*, *Manuelophrya*, *Rhynchophrya* and suctorians ascribed to *Sphaerophrya* or *Podophrya*; in seawater, we can meet *Endosphaera*, *Pseudogemma*, *Ophryocephalus*, *Pottsiocles* and *Tachyblaston* (detailed review in Jankowski 2007). *Ephelota*, a large exogemmic suctorian common in marine periphyton (especially on hydroids), may bear 4 such suctorian parasites – *Acinetopsis*, *Ophryocephalus*, *Pseudogemma*, *Tachyblaston,* and may be infested by hypocomids; they occupy different loci on the host. These hypocomids are shown by Chen et al. (2008), but are treated by mistake as swarmers (separated basal buds) of *Ephelota truncata*, different from the true apical ephelotid buds shown in their drawings of *E. gemmipara*.

I have spent several summers on Lake Baikal in Listvenka region (where mighty river Angara, 1 km wide, flows out of the lake), and also participated in several trawling voyages on ships of the Limnological Institute (then in Listvenka, now in Irkutsk). Extensive suctorian material was examined – periphytonic, commensal and parasitic suctorians; during these studies, I have found a variety of symbionts – *Sphaerophrya* on stentors and vorticelles; *Riftus* on colonial peritrichs; *Endosphaera* in a modified vorticellid *Spongostena*, in the true *Vorticella* and in *Pseudovorticella* with water-filled alveoli (*P. vestita*); an unexpected *Endosphaera* in *Dendrocometes*; *Mistarcon* on *Epistylis*; *Erastophrya* on *Apiosoma* living on fishes; *Urnula* on *Stylophrya*, pathogenic to its suctorian host; *Gajewskajophrya* on pelagic diatoms; endemic *Tokophryona* on *Anabaena*, and suctorians on oligochaetes, copepods, ostracods and amphipods.

Colonies of *Carchesium* are common everywhere in Listvenka region, but a special search has never revealed its common European symbiont *Tokophryella carchesii*. Instead, in a rapid shallow cold mountain river in Krestovka Valley, full of large boulders and practically devoid of any animal or plant life, the underside of boulders bears rare colonies of *Carchesium* with strange new symbionts – large modified metacinetids. They were noted during my last visit in 1998, but were not studied and repeated visit to Baikal was not later possible. On Angara river shores, the underside of boulders bears mainly *Acineta* (subgenus *Acinetella*), *Vorticella* and *Carchesium*. Vorticelles are infested with *Sphaerophrya*, perhaps *S. epizoica* (= *Podophrya epizoica* Hammann, 1952), described in Germany from several peritrichs, with their main host being *Vorticella campanula*); and many cells of *Vorticella* are dead, but not disintegrated, with a growing 2-horned fungal sporangium inside; open horns protrude out of the cell and serve for liberation of numerous flagellated spores. This parasite differs from fungi described before as parasites of peritrichs. *Carchesium* here bears small vorticelles on its stems (a new undescribed species) and is occasionally infested with these fungi and *Sphaerophrya* from their main host – vorticelles, growing nearby.

Until a relatively recent introduction of *Elodea canadensis,* there were no plants in the near-shore waters of this region in Baikal, only bushes of tiny filamentous green algae *Ulothrix*, covering stones as a dense algal mat, and practically free of epiphytes, unlike shallow estuary of the Selenga River on the opposite shore, filled by flowering plants with rich periphyton on them. These plants are not seen from the shore and are shifted deeper from the surf area; after autumn storms the near-shore waters are replaced by mighty ice during winter and long frosty spring, thus excluding growth of any submerged plants in the littoral area. *Elodea* may be collected in summer by divers; this was not possible for me, and I collected these plants washed ashore after storms in September 1997 and 1998. Surface of large leaves was heavily populated by a rich variety of diatoms (partly infested with the smallest external parasites, sucking their cytoplasm through a slit in the shell), cyanobacteria, filamentous algae, and numerous sedentary ciliates. Colourless stentors (*Stentor roeselii*, *S. polymorphus*) are infested with *Sphaerophrya* of the usual type, like those in *Paramecium*; spherophryids with a unique type of fission or those with atypical thick conical tentacles, infesting other species of stentors, were not noted in these two hosts. Orange *Hydra*, occurring on stranded *Elodea*, is different from light-brown or beige *Hydra* in shoreline ponds and streams, and is commonly infested with *Tetrahymena*, swimming freely in body fluids inside the body stem and tentacles – perhaps "*Balantidium*" *hydrae* Entz, 1912 (*Tetrahymena hydrae* comb. nov.) that will be redescribed. Two other symbionts accompanying *Hydra* in Europe and USA (hypotrichs *Kerona* and mobilids *Trichodina*) were absent on both hydras examined in this region. Likewise, mobilids *Trichodina* and *Urceolaria* and intestinal astomes *Sieboldiellina* with anchoring hooks, widespread in Europe, were never found in Baikalian planarians, and small asellotes here do not carry shelled peritrichs *Usconophrys* and *Lagenophrys*, but these symbionts, common on European *Asellus aquaticus*, reappear on Far East on *A. hilgendorfi* (my samples in South Sakhalin). A lack of some common Palaearctic symbionts in Baikal is evident reality, as well as radiative evolution of other symbiotic ciliates, associated with endemic worms, molluscs and amphipods in this lake.

Carchesium is common in local periphyton; as noted above, no specimens of *Tokophryella carchesii*, well-studied in Europe, were found, but instead small suctorians are attached to upper branches of the colony, sometimes up to 60 symbionts per colony of a host. Other symbionts are small short-stalked *Vorticella*, attached to branches of *Carchesium* and entirely covered by rod-like epibacteria, except a smooth retractile peristomal disc; in contrast, none such bacteria are present on zooids of *Carchesium* of the same colony, thus indicating the rigid specificity of these epibacteria to vorticelles. Such dense cover of bacteria is more common in seas (on *Dysteria*, *Sonderia*, *Parablepharisma*, *Metopus*, *Zoothamnium*, *Ephelota*, and famous "bacterial garden" on primitive vermiform ciliate *Kentrophoros*). Association of *Carchesium* with epibiotic *Vorticella* is known in the previous literature, but the species have not yet been described and named. Suctorians found on *Carchesium* are described below as a new species and genus, supposedly of the family Tokophryidae.

MATERIAL AND METHODS

Research was made in summer, when storms were rare, and in autumn, with frequent storms, in 1997 and 1998 in Listvenka region, south-west Baikal. A large area was surveyed along the Angara River and on both sides of Listvenichniy Bay (shores of Listvenka and of Port Baikal on the opposite side of the Angara outflow); this area can be seen in detail using a "Google–Earth" Internet program. *Elodea* was washed ashore only in a very limited region – on small sandy beach, near 100 m long, northwards from the wharf (pier) of Listvenka. When storms were quieting, plants were collected and immediately fixed with 5–8% formalin or in half-diluted Bouin's fluid until the end of their stranding; the last ones were transferred intact in pure water to laboratory, 2 miles away, for study of living material. Attached ciliates on stranded plants were better retained during rains, otherwise drying of *Elodea* with its periphyton was very rapid.

Large bush-like colonies of *Carchesium* were easily separated from fixed plants and were retained individually in small 1 or 1.5 ml plastic centrifuge tubes. Material thus fixed was studied in 2008; the cytological state of cells was perfect. Fragments of colonies, unstained or in acidified methyl-green with subsequent washing of excess of stain, were located in a small drop of diluted formalin in the centre of a microscope slide and surrounded by a ring of vaseline oil (= paraffin oil) coloured by a lipoid stain (Sudan Black was only available; it gives violet tint to the oil). When a thin coverglass is placed over the drop, the drop with material is surrounded by violet oil and the preparation thus framed can be stored many months, to year or more, but not permanently because water slowly evaporates through oil by a mechanism of molecular migration. This can be verified, if we put the smallest drop of pure water, formalin or salt solution on a slide, and cover it with vaseline oil; it will dry out in 2–3 days under a thin layer of the oil and a salt or polymerized formalin will crystallise. Permanent slides were made in a standard way – colonies stained by nuclear stains (toluidine blue, basic fuchsine) after hydrolysis in 10% HCl were gradually transferred through dioxan to Canadian balsam and mounted under a thin coverglass.

A single drawing can be made by free hand or with the aid of a bar or ocular micrometre, but a large series of drawings requires exact proportions. I used a method with an ocular reticle (16 × 16 squares) that permits the exact drawing of a small ciliate (30–50 µm) on the entire sheet of A4 paper. All drawings of *Irkana linica* in this article were made at 7 × 90 magnification, with a reticle within ocular ×7. A series of drawings is made on the identical set of sheets and thus reflects growth stages and individual variation of ciliates better than standard morphometric tables; many drawings give impression of a range of individual variation without the need to select one "typical" cell. It may seem that a higher number of lines on the sheet makes drawing easier, but identification of squares is difficult when their number exceeds 10. I guess that 10 × 10 reticle, commonly used abroad, is more useful for drawings of protozoans under oil immersion.

SYSTEMATICS

Class Suctorea Claparede et Lachmann, 1859

Order Acinetida (authorship is disputable; see Jankowski 2007: 705)

Family Tokophryidae Jankowski, 1978

Genus *Irkana* Jankowski gen. nov.

Diagnosis. Small ovoid bag-like endogemmine suctorians with simple ovoid macronucleus; extensible capitate tentacles ("*acrotenes*") are not confined to distinct hemispherical actinophores, unlike *Acineta* and *Tokophrya*, but project from the body surface and show some tendency to form 2, 3 or rarely 4 indistinct bundles. Adhesion by homogenous disc, with no trace of stalk or its rudiment (pedicle). Symbionts on stems (contractile branches) of colonial peritrich *Carchesium* in Lake Baikal, never attached to zooids themselves; parasites sucking host zooids. Type species by monotypy *Irkana linica* sp. nov.

Irkana linica Jankowski sp. nov.
(Figs. 1–47)

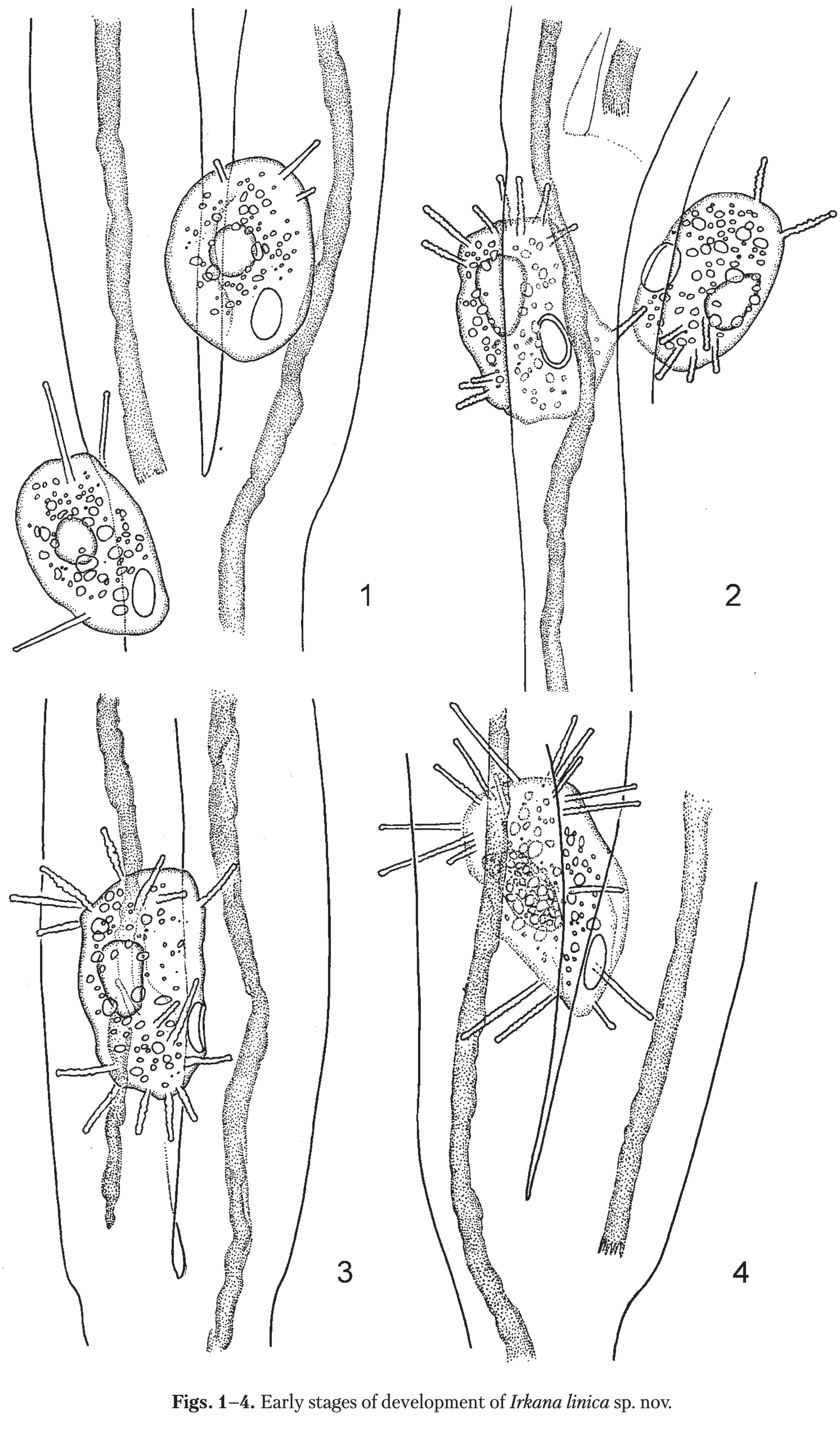
Type material – 12 slides, one of these designated as hapantotype (No. 2008–5), each with one colony of *Carchesium* bearing parasites. Peritrich colonies are stored in glycerine to prevent drying; the frame is made by a ring of black asphalt lac around the glycerine drop. Although less refractile than in formalin, suctorians and host zooids are clearly seen and structural details (nucleus, tentacles, fixon) can be studied under oil immersion. Slides are stored in the Laboratory of Protozoology, ZIN, Anglijskij Prospekt 32, Saint Petersburg, Russia.

Etymology. There are river and lake Irkana in northern Baikal region, bay Irkana within Chivyrkuy Gulf, small tourist ship "Irkana" for travels along the shores, but the new genus bears the name of a beautiful large sail-diesel yacht "Irkana", that was always present at the sampling site in Listvenka during autumn storms. Species name "*linica*" – from LIN, Limnological Institute SB RAS (now in Irkutsk).

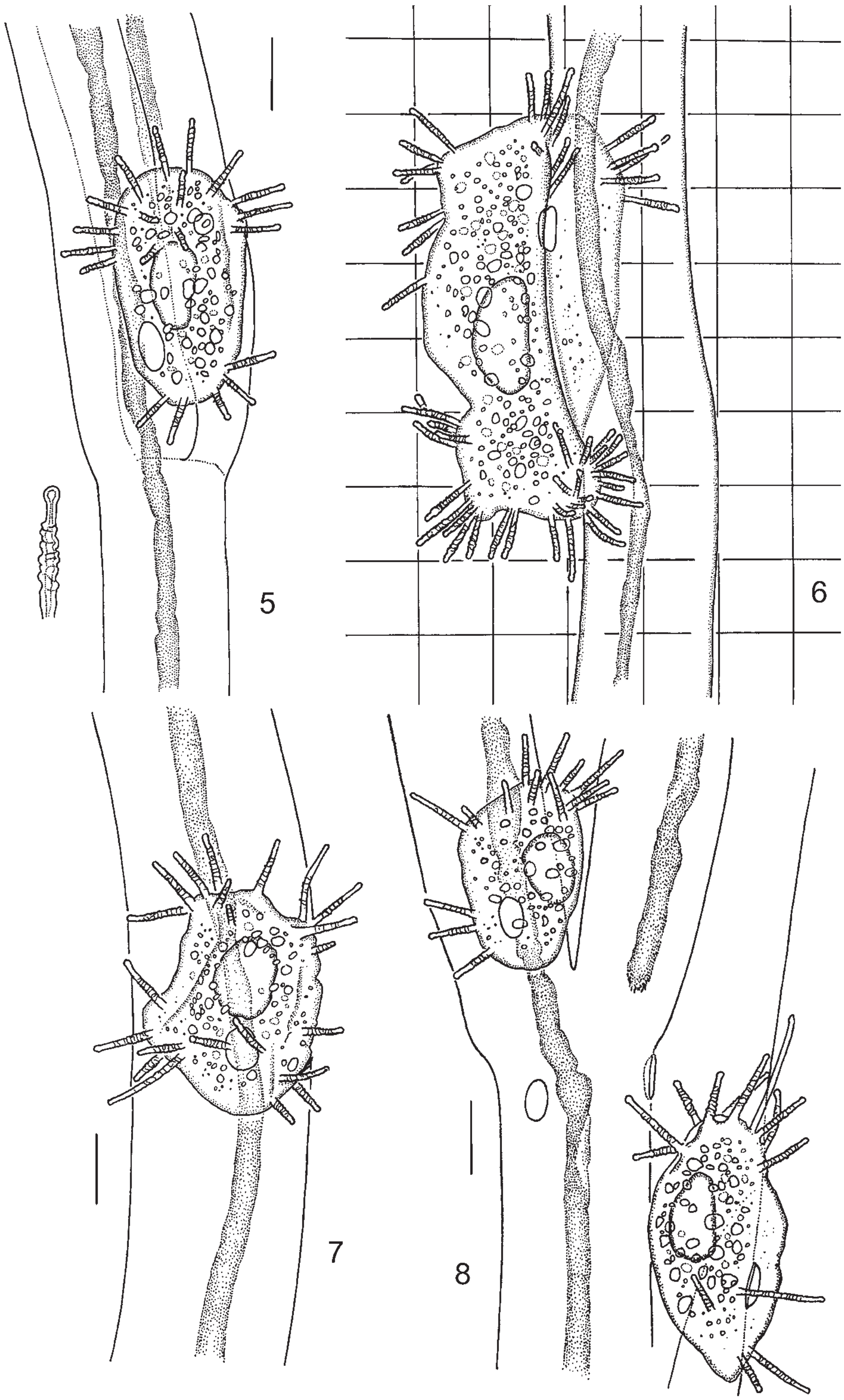
Morphology. Zooids of these suctorians are well seen at low magnification as dark spots on branches of *Carchesium*, separated from *Elodea* leaves; body ovoid, distinctly elongated, variable in shape, usually with convex upper side and concave lower part adjoining to host stalk. The cells are firmly fixed on this substratum by ovoid "*fixon*" (my term for adhesive structures in ciliates except what may be called the true stalk; very short stalk, pedicle, disc or any other secretion is fixon). Fixon is structureless, clear and homogenous, with a high refraction index. Although stranded material was collected during storms, numerous ciliates were firmly fixed on hosts by this fixon; we can also find fixons without ciliates (Figs. 8, 38, 39). Fixon of *Irkana* does not resemble basodisc (attachment disc) or epidisc (the wide upper part of the stalk below scopula) of *Tokophrya*, it may be a special secretion, not the rudiment of the stalk. Macronucleus central, round to ovoid, densely granular (Figs. 4, 15); micronucleus small, round, near 1.2 μm in diameter.

Tentacles long (up to 45–68 mm) and straight when extended, folded at contraction, with distinct elongated or round apical cup; I call this type of tentacles "*acrotenes*", they are typical for *Acineta* and *Tokophrya*. The cell may have up to 40 tentacles in total, usually less; distinct refractile homogenous hemispherical actinophores, typical for named genera, are absent in *Irkana*; tentacles rise from the body surface in a somewhat erratic pattern, with tendency to grouping into 2, 3, rarely 4 indistinct bundles. Figs. 1–37 and 40–47 show variation in number and position of tentacles from early stages to adults. It might be expected that the adults have the largest number of tentacles, but, inversely, the largest cells have few tentacles (14 and 8 in Figs. 46 and 47). Supposedly, *Irkana* feeds on zooids of the host with the aid of its extended tentacles, like two other similar parasites of colonial peritrichs – short-stalked *Tokophryella* and *Riftus* with a similar fixon.

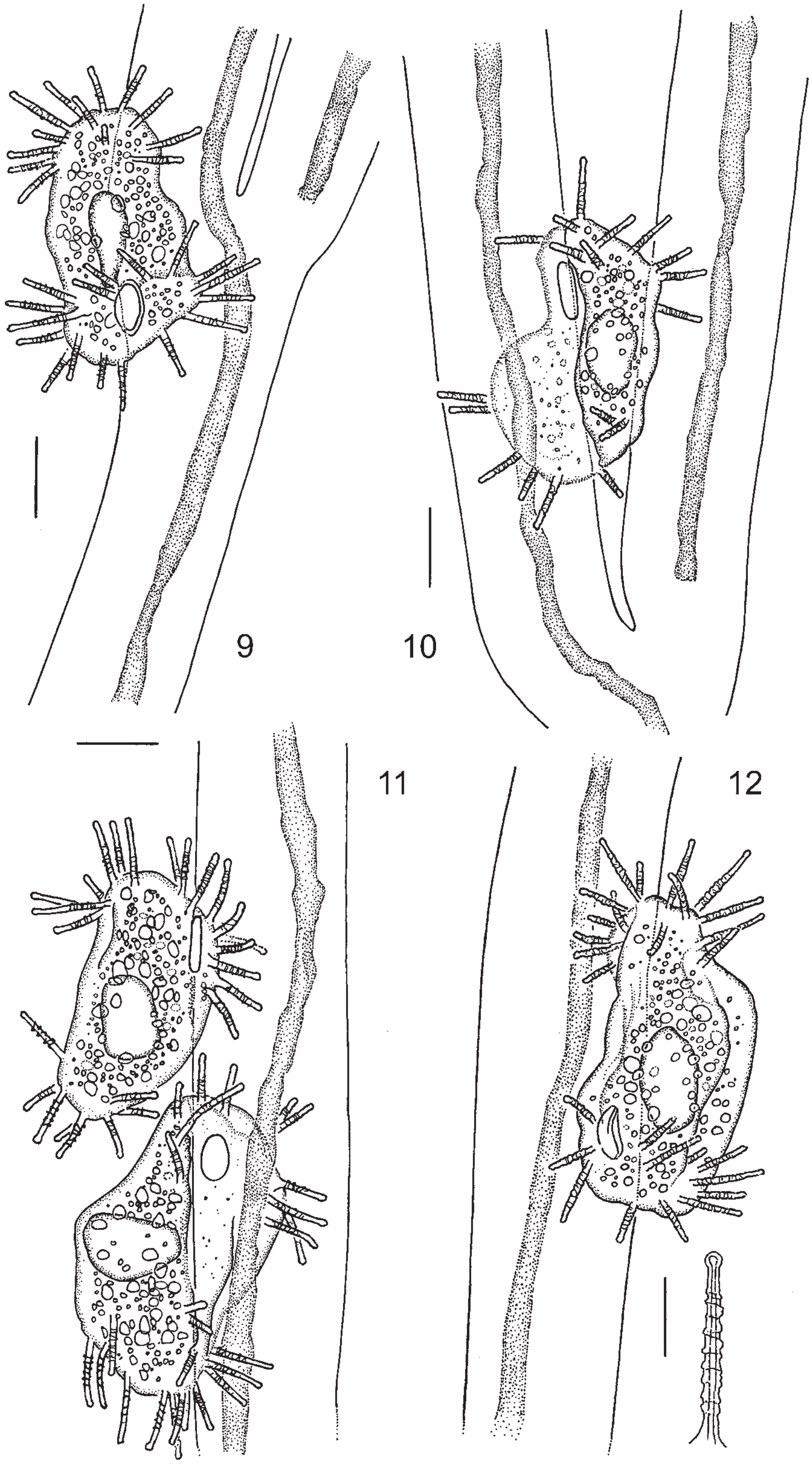
In spite of the extensive material fixed directly on the shore, I have found only one tomont with a small internal bud (Fig. 30). This specimen may explain cell orientation – in acinetids and tokophryids, tomite is made under cell apex (right side of the drawing), opposite to the posterior part (fixon); upper and lower edges with tentacles are left and right sides of the cell. *Irkana* can be a modified *Tokophryella* with a loss of the stalk and a lateral extension of body sides with tentacles. Dimensions of cells (40 measurements un-



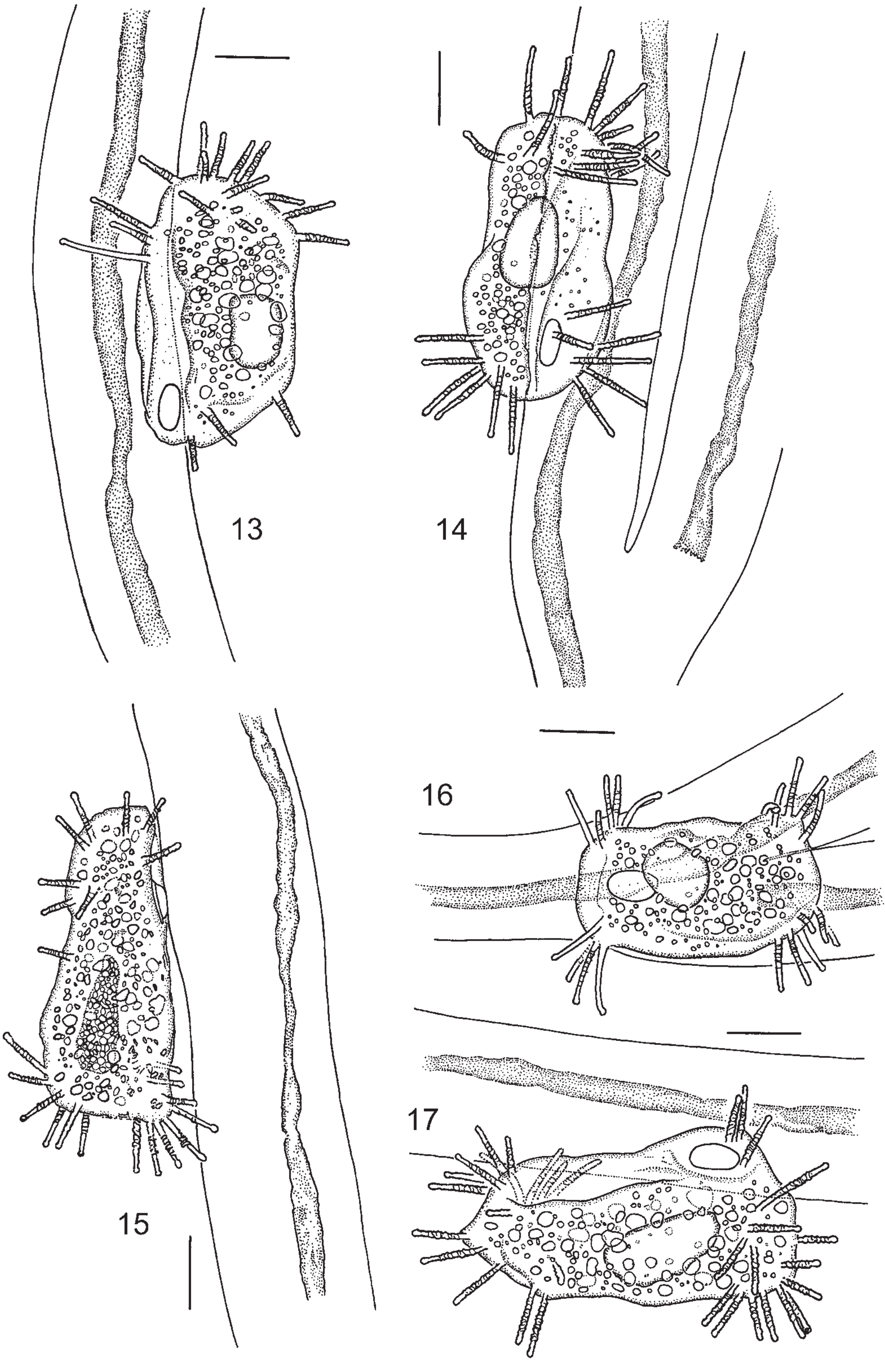
Figs. 1–4. Early stages of development of *Irkana linica* sp. nov.



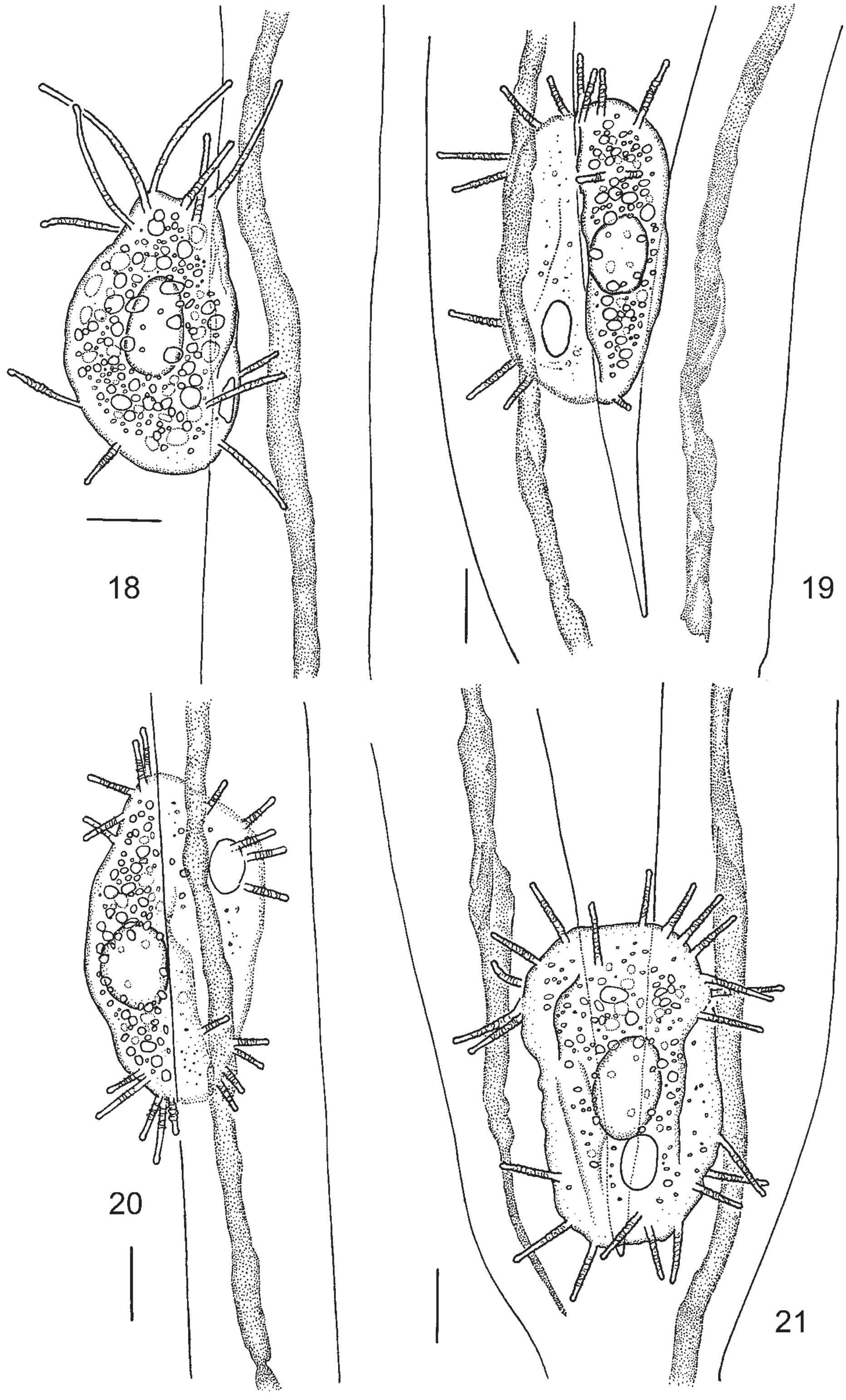
Figs. 5–8. *Irkana linica* sp. nov. 5, 7, 8 – young trophonts; 6 – well-fed trophont. Method of drawing – on a A4 sheet with a pencil reticle of 3 cm between horizontal and vertical lines (erased on trophont); oil immersion, 7 × 90, with a reticle of 16 × 16 squares in ocular ×7. All drawings except Figs. 38, 39 and 48 were made in the same way. Scale bar 10 μm.



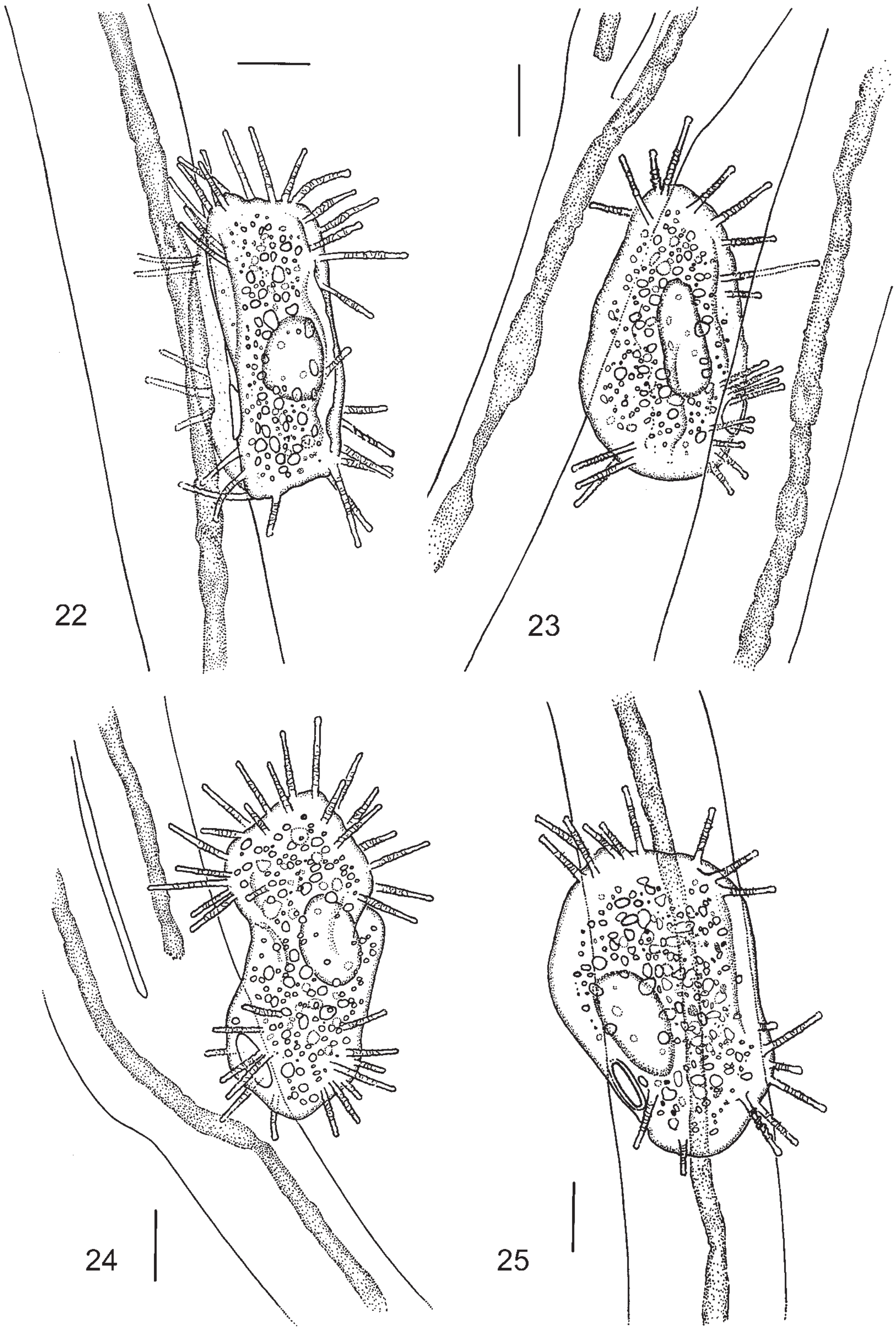
Figs. 9–12. Growing trophonts of *Irkana linica* sp. nov. Scale bar 10 μm.



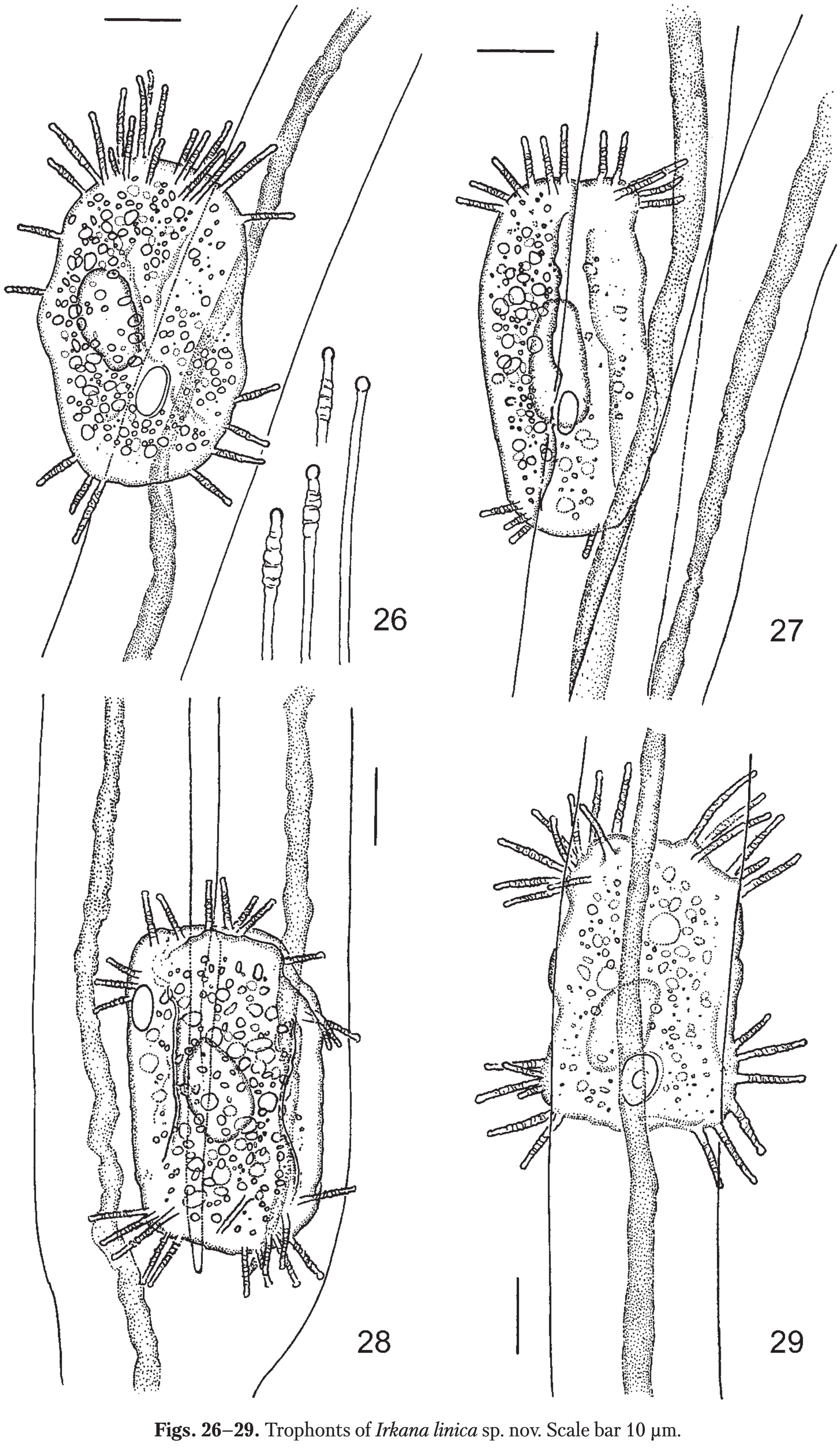
Figs 13–17. Growing trophonts of *Irkana linica* sp. nov. Scale bar 10 µm.



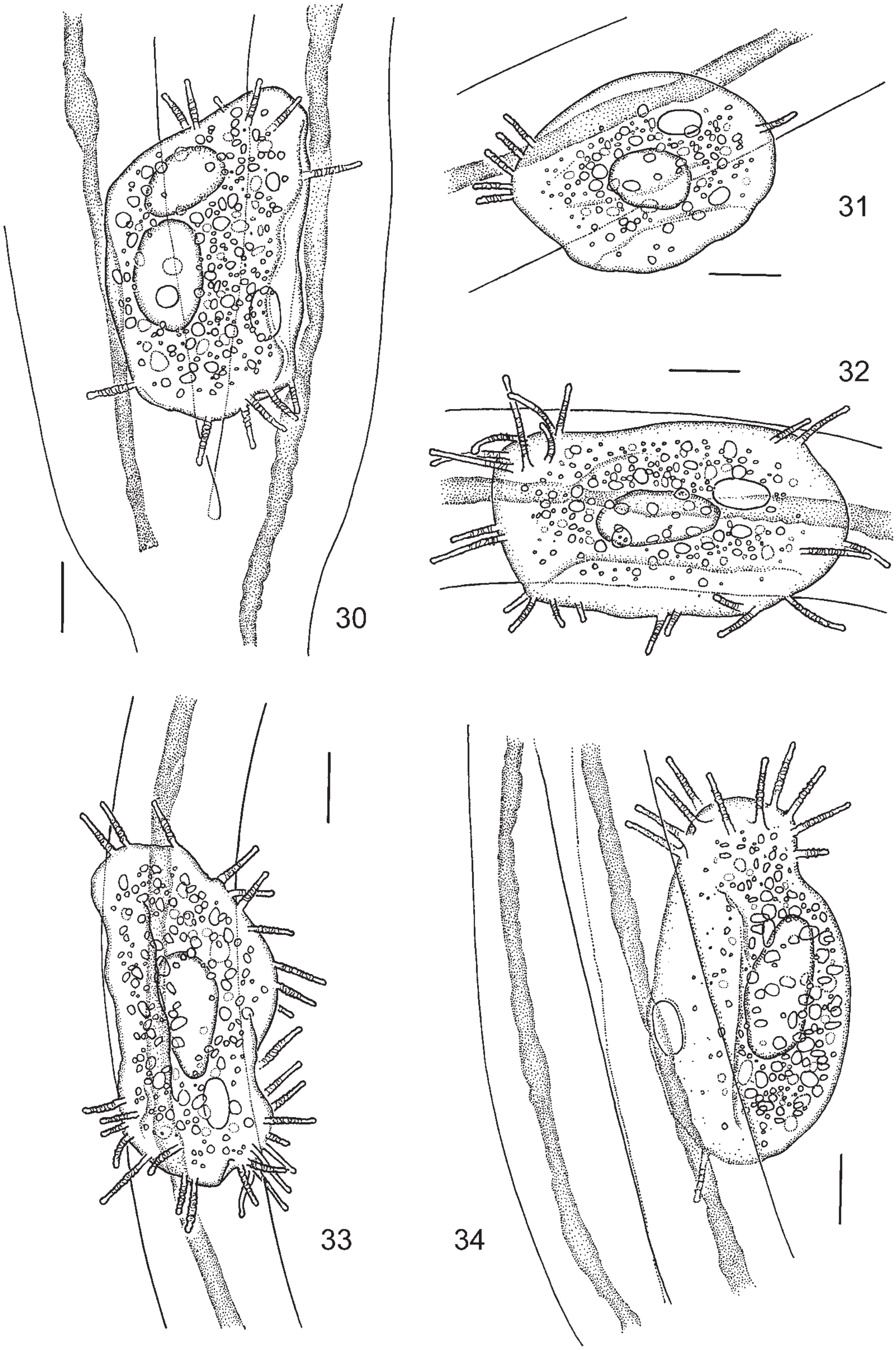
Figs. 18–21. Growing trophonts of *Irkana linica* sp. nov. Scale bar 10 μm.



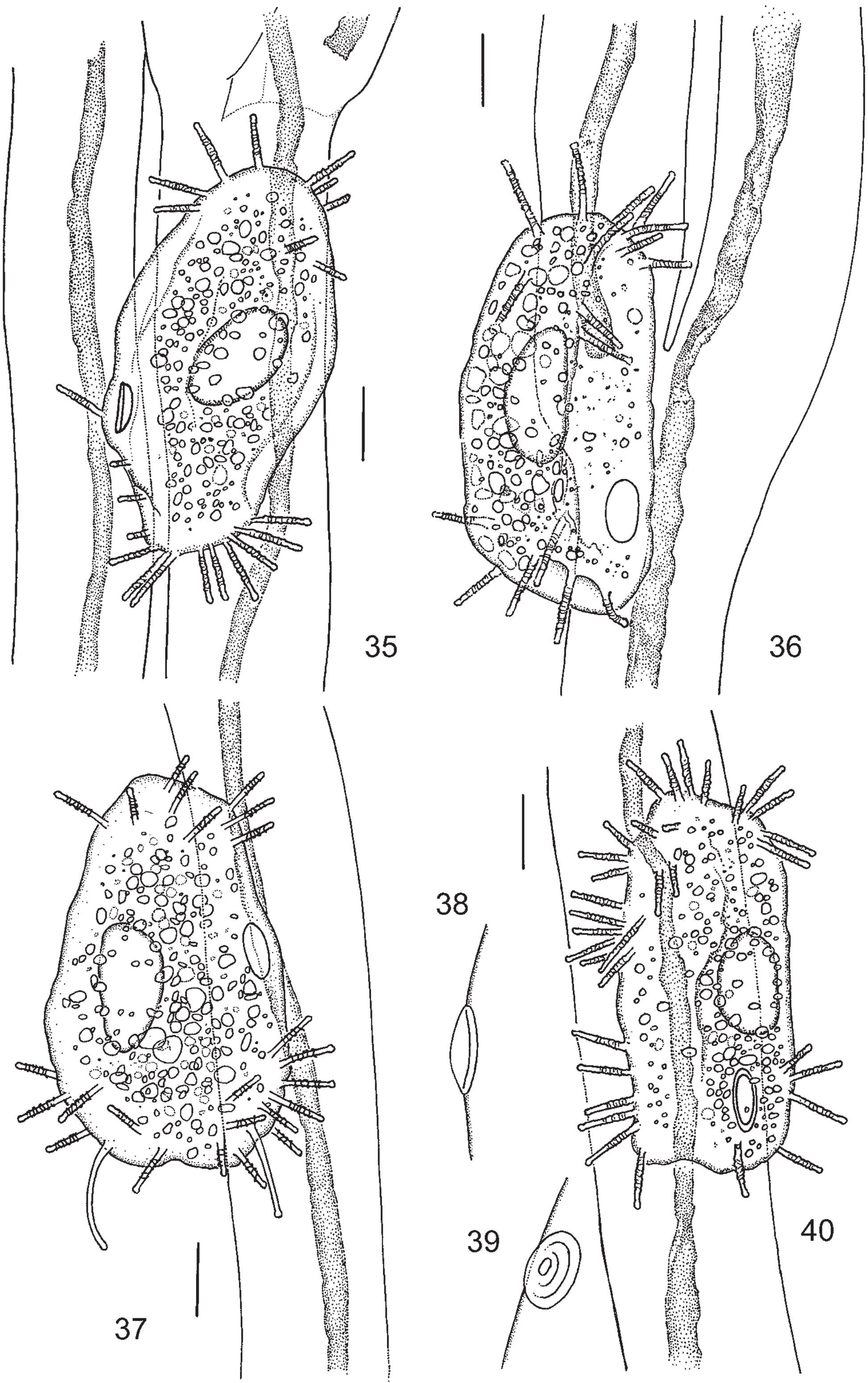
Figs. 22–25. Growing trophonts of *Irkana linica* sp. nov. Scale bar 10 µm.



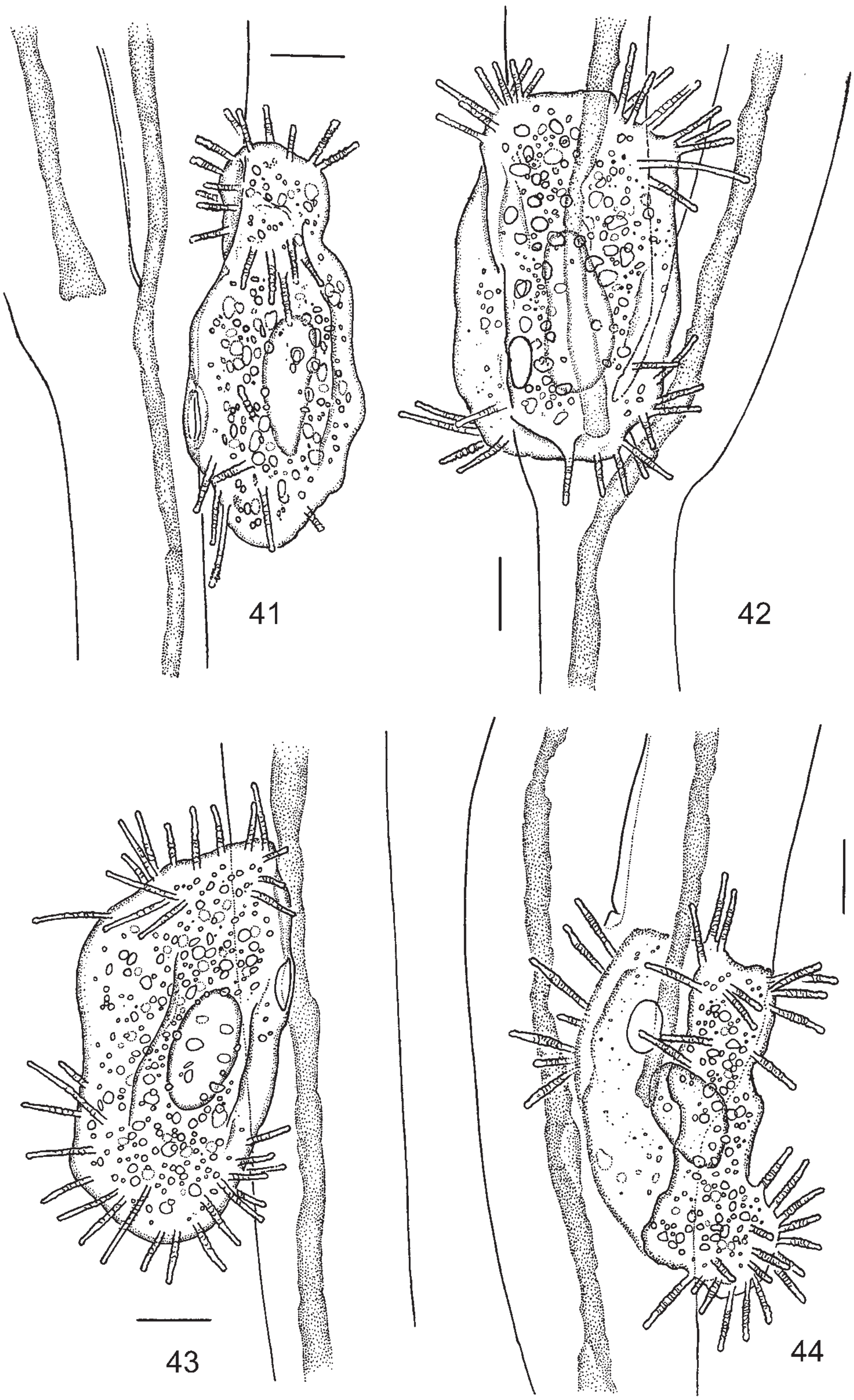
Figs. 26–29. Trophonts of *Irkana linica* sp. nov. Scale bar 10 µm.



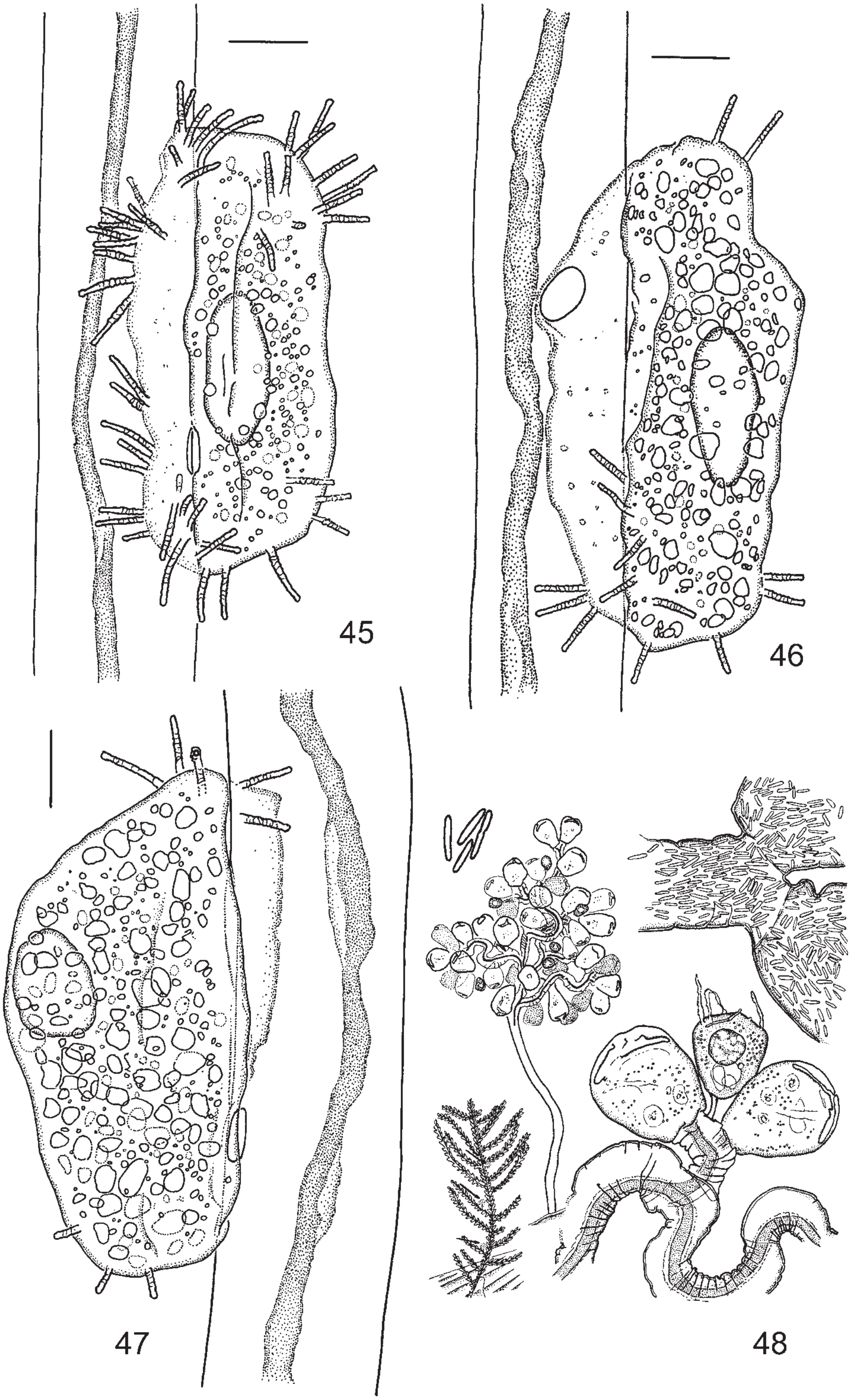
Figs. 30–34. Trophonts and tomont of *Irkana linica* sp. nov. Scale bar 10 µm.



Figs 35–40. *Irkana linica* sp. nov. 35–37, 40 – trophonts, scale bar 10 μm; 38, 39 – two fixons from detached cells, drawings without scale.



Figs. 41–44. Adult trophonts of *Irkana linica* sp. nov. Scale bar 10 µm.



Figs. 45–48. 45–47 – largest trophonts of *Irkana linica* sp. nov., scale bar 10 µm; 48 – small acinetid suctorians (dark spots on the host colony and one enlarged cell) and bacteria on the contractile stalk of *Zoothamnium* sp. growing on hydroid *Obelia* on a scallop shell, Barents sea; free-hand drawings without scale.

der oil immersion, 90 × 10) 34–72 µm, macronuclear size 10–22 × 6–9 mm, contracted tentacles 4–12 µm long, size of adhesive disc (fixon) 6.5–7.2 mm. The sizes of branches of *Carchesium* are not equal, they may be thin or thick, muscles are acute after bifurcation of the stalk and become wider as the colony grows; this is evident in drawings made with reticles in the ocular and on paper, with coinciding proportions. The width of host stalks varies from 17 to 27 µm. The upper branches are main sites of adhesion, mostly near bifurcation points.

Host. Two species of *Carchesium* occur in the sampling area; colonies with small zooids on the underside of sublittoral stones are typical *C. polypinum* (Linne, 1758) Ehrenberg, 1831, they never bear *Irkana*; those on *Elodea* have large zooids and can be identified as *C. wassenum* Viljoen et Reinecke, 1988.

DISCUSSION

The new symbiont is morphologically unique, and I have almost nothing for comparison. No other tokophryid suctorian, except *Riftus*, has such fixon – refractile homogenous disc, but a similar fixon was detected in the youngest growth stages of *Trichophrya*. There are no actinophores, and tentacles are not in a single apical bundle. No trace of shell or "epitheca" can be detected; "*epitheca*" is my term for rigid epicuticle, firmly adjoining to the cell membrane (such as will be shown in my prepared articles on *Acineta fluviatilis* and on a new species of *Tokophrya* from frogs). *A. fluviatilis* has such epitheca on the entire body, never detached from the cell, except anteriorly around actinophores and between them; thus *Acineta* may be split into 2 genera – with true shell, almost completely detached from zooid, and with epitheca and apical shell walls in *A. fluviatilis*, intermediate between *Tokophrya* and shelled *Acineta*. Such rigid cell cover (epitheca) is known in many other phylogenetically unrelated ciliates, like *Pseudomicrothorax*, *Epalxella*, *Sonderia*, in rumen entodiniomorphs.

For *Riftus*, the following text is a translation from my annotated checklist of ciliate genera (Jankowski 2007: 711). "Genus *Riftus* Jankowski, 1981. Type species *Discophrya pygmaea* Swarczewsky, 1928 – epibiotic species on stalks and branches of colonial peritrichs *Zoothamnium* sp. on gammarid *Pallasea bicornis* from 40 m depth in Baikal; my material – from large colonies of *Zoothamnium* sp. on pereopods of *Acanthogammarus victorii* from depth 70 m. Zooid of type race pyriform, narrowing to base, attached by short wide stalk; with numerous acrotenes over entire upper hemisphere; with internal embryo. In my material (Jankowski 1981, 1982; the genus was twice established as new) stalk is absent, tentacles are flexible; with tips like in acrotenes, but folded and thickened below at contraction. Both species look different, but I am sure that the drawing of the type race was incorrect. The genus *Riftus* is regarded as a synonym of *Tokophrya* sensu lato; the species is approached to *T. carchesii* (see *Tokophryella*), but is not synonymized with it; but according to the position of tentacles (entire apex) this is a valid subgenus or genus".

Riftus is treated as a valid genus of endogeneans, aside with *Rhyncheta*, by Dovgal (2002). Genera differ in body shape and position of tentacles, apical in *Riftus*, but on the opposite sides in *Irkana*. Clear lower body part of *"Discophrya" pygmaea*, devoid of grains, was regarded by Swarczewsky (1928) as a short wide stalk, absent in all specimens examined on my slides under oil immersion. The same mistake is repeated on Swarczewsky's drawings of *Acinetides*. Slides of that author, examined by me in Irkutsk, are stained by pale carmine, faded with time, and a thick layer of balsam does not permit study under oil immersion. Curds (1985) includes this species as *Tokophrya pygmaea* in his checklist of *Tokophrya*, and this decision is based on the incorrect original drawing of this small parasite.

Tokophryella carchesii (= *Podophrya carchesii* Claparede et Lachmann, 1859), usually in *Tokophrya*, is a small suctorian with a pyriform or drop-like body, few apical tentacles and short stalk with distinct basodisc; some specimens are asymmetrical, tentacle bases are shifted aside, rarely to an almost lateral position. Tentacles are extremely extensible, for sucking of remote zooids of the host colony. The type species of the genus *Tokophrya* is monstrous *T. quadripartita*, with 4 actinophores on the wide apex, and the small parasite with few apical tentacles in a single bundle can be separated from species with 4 and 2 tentacles (the majority of tokophryans) at least as a subgenus. *Irkana* and *Riftus*, both attached to contractile stems of peritrichs, may be independent derivates of *Tokophryella* at a loss of the stalk. *T. quadripartita* is commonly associated with large colonies of *Epistylis plicatilis* growing on shells of small planorbids.

Is *Irkana* endemic of the lake? Small enigmatic suctorian *Sphaerophrya melosirae* Gajewskaja, 1933 (now type species of *Gajewskajophrya* Matthes, 1988), attached to pelagic diatoms *Melosira*, was regarded previously as Baikalian endemic, but later it was found in Europe (see coloured micrographs and description in Foissner et al. 1999). Holotrich ciliates *Marituja* and *Sulcigera* were also in lists of endemics of the Baikalian plankton, but now are found in Europe (peniculid *Marituja*) or synonymized with the common pleuronematid *Histiobalantium*. On the contrary, Baikalian benthos is rich in endemic ciliates. Until it will be found outside the lake, *Irkana*, *Riftus* and *Tokophryona* must be regarded as endemics of Baikal, a unique deep rift lake with at least 10 million years of existence.

Fig. 48, from my old unpublished archive, is a free-hand drawing of small acinetids inhabiting colonial peritrichs *Zoothamnium* sp. on hydroids growing on pectenid bivalves (scallops *Chlamys islandicus*) trawled in the Barents Sea; this association was not studied, but acinetid is surely new. These symbionts are seen as dark spots on the host colony, one of them is enlarged. Thus similar host-specific associations of small suctorians with retractile colonial peritrichs exist both in fresh waters and seas.

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