

Studies on monad flagellates.

I. Historical and taxonomic review of the genus *Monas*,

II. Observations on *Monas vestita* (STOKES, 1885).

By

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(With 3 figures in the text and plate 12.)

I. Historical and taxonomic review of the genus *Monas*.

The family Monadidae comprises a number of small flagellates, characterized by having a flexible surface and two unequal (one primary and one secondary) anteriorly directed flagella. Some are single and naked, *Monas*; single and loricate, *Stokesiella*; colonial and naked, *Anthophysa*; colonial and loricate, *Stylobryon*. Some species are characteristically free-swimming while others are generally attached - though individuals of all species may break away from their mooring and swim away. They have been reported from both fresh and salt water; in either case, however, they are more common in old infusions.

The genus *Monas* was established by O. F. MÜLLER (1773), its representatives being defined by him merely as punctiform organisms. Dujardin observed the primary flagellum, apparently for the first time, in 1835. EHRENBERG defined representatives of this group as being destitute of an eye; mouth near anterior end; a single filament, issuing from near the mouth, serving both for locomotion and for procuring food. STEIN (1878) emended the generic definition so as to include only small spherical or elongated forms; free-swimming or attached at the posterior end by means of a pseudopodlike thread; body occasionally somewhat amoeboid; one primary flagellum and one or two accessory flagella; mouth-streak and also an eyespot occasionally present; nucleus in fore end of body; one or two con-

tractile vesicles; food taken in through a mouth-vacuole near base of the flagellum. It has not been necessary to alter this definition materially up to date.

O. F. MÜLLER (1786) very imperfectly described ten species of *Monas*. According to DUJARDIN, at least two of these, *M. termo* and *M. punctum* were bacteria. BORY (1824)¹) recorded several species. EHRENBURG (1838) listed twenty-eight species under this generic name. This list includes some of the specific names of MÜLLER. Owing to his inadequate descriptions, however, it is impossible to be certain as to identity. Though questioning the validity of some of EHRENBURG's species, DUJARDIN (1841) described twelve new species of *Monas*. PERTY (1852) added eleven more; and FRESINEUS (1858) four. PRITCHARD (1861) records fifty-five species, though no new ones are described. FROMENTEL (1874) contributed three new species to the long list, but it is evident that he did not thoroughly acquaint himself with literature on the subject; and as his descriptions are inadequate, it is difficult to know whether or not he was dealing with new organisms. KENT (1880) added five new species, recorded twenty-six old species and listed twenty previously described species which he considered to be of doubtful validity.

It will be noted that some seventy or seventy-five species had been referred to the genus *Monas* by the year 1880. The earlier investigators included many bacteria, as well as divers flagellates, in this group. EHRENBURG (1838), DUJARDIN (1841) and others observed the primary flagellum and, generally, considered these organisms as uniflagellates. CIENKOWSKI (1865) and STEIN (1878) included forms with one, two and three flagella. KENT (1880) gives a lengthy discussion of the genus *Monas* in which he contends that this generic name should be restricted to those organisms possessing only one flagellum. On this basis he refers *Monas guttula* EHRENBURG to the genus *Spumella* created by CIENKOWSKI. BÜTSCHLI (1883) states that members of this genus possess one primary flagellum and one or two secondary flagella. He considers CIENKOWSKI's genus *Spumella* to be a synonym for *Monas* and, accordingly, puts *Spumella guttula* (EHRENBURG) KENT back into the genus *Monas*.

STEIN (1878) seems to have been the first to start the process of splitting up the old genus *Monas* on a large scale. He created new genera for some and transferred others to already existing genera. For example: *Cercomonas termo*, *Spongomonas consociata*,

¹) I did not have access to this publication.

Raphidomonas serum, *Chrysomonas flavicans*. He mentions only two species of *Monas* viz: *M. vivipara* and *M. guttula* (*Spumella vulgaris* CIENK.) BÜTSCHLI (1883) follows STEIN in regard to the genus. LEMMERMANN (1914) in Heft 1, Die Süßwasserflora, lists the following species:

Monas vivipara EHRENBERG

Monas vulgaris (CIENK.) SENN. (This is probably a synonym.)
(for *M. guttula* EHR.)

Monas gelatinosa NÄGLER

Monas Dangeardii LEMM.

Monas arhabdomonas (FISCH) H. MEYER

Monas minima H. MEYER

Monas obliqua SCHEWIAKOFF

Monas elongata (STOKES) LEMM.

Monas socialis (KENT) LEMM

Monas amoebina H. MEYER

Monas sociabilis H. MEYER

PASCHER (1918) cultivated a species of *Monas* which sometimes would quickly resorb its flagella and become amoeboid. He called it *Monas amoeboidea*. From the pictures it appears to belong to that genus. No description is given.

GICKLHORN (1920) describes a form under the name *Monas micropora*. It is quite obvious from his descriptions, as well as from his drawings, that he was dealing with several different protozoa. His drawings depicted in Text-Fig. 1 d, e, f, g, h and i represent a species of *Salpingoeca*. His descriptions and drawing Text-Fig. 1 a do not differ materially from *M. Dangeardii* LEMM. The organism pictured by him in Text-Fig. 2 has certain characteristics of the one described in this paper. It is highly improbable, however, that it is connected with the form which he described as *M. micropora*. He says of it: „Über die Beziehung zu unserem Eisenflagellaten kann ich nichts weiteres angeben; möglicherweise ist es jenes Stadium, wo Teilungen eingeschaltet werden.“

The evidence presented by GICKLHORN is inadequate to justify the establishment of a new species and consequently, *M. micropora* should not be recognized.

The flagellate described under the name of *Sterromonas formicina* by KENT (1880) should be transferred to the genus *Monas* and, in my opinion, become synonymous with *Monas guttula* EHR. This opinion is expressed in part, by BÜTSCHLI (1883) and GRIESSMANN (1914).

KENT's principal reason (aside from the possession of two flagella of unequal size) for creating the genus is based on the fact that the long flagellum remained constantly rigid near its base. This is a common characteristic of many members of the genus *Monas*. This leaves no species in the genus *Sterromonas*.

The genus *Physomonas* was established by KENT (1880) to contain a stalked monad possessing two unequal flagella, which he called *Physomonas socialis*. This species has been transferred to the genus *Monas* by LEMMERMANN (1914). STOKES (1885) described as *Physomonas vestita* an organism which he found growing in pond water with *Myriophyllum*. In addition to a stalk three to four times the length of the body, this flagellate was covered with a layer of mucus from which numerous fine threads radiated. In other respects it is like representatives of the genus *Monas*. Owing to the fact that many species of *Monas* may become attached by such a stalk and furthermore since at least one species, *Monas gelatinosa*, is enveloped in a gelatinous covering, there seems to be no valid reason for not putting this organism in the genus *Monas*. This removes the last representative from the genus *Physomonas*.

To summarize then: 1. *Monas vulgaris* (CIENK). SENN is a synonym for *M. guttula* EHRENBURG. 2. *M. micropora* GICKLHORN is inadequately identified and, therefore, should be suppressed. 3. *Sterromonas formicina* KENT is a synonym for *M. guttula* EHR. 4. *Physomonas vestita* STOKES should be transferred to the genus *Monas*. The genus *Monas* as thus revised comprises the following thirteen species: *M. amoebina* MEYER, *M. amoeboidea* PASCHER, *M. arhabdomonas* (FISCH) MEYER, *M. Dangeardii* LEMM., *M. elongata* (STOKES) LEMM., *M. gelatinosa* NÄGLER, *M. guttula* EHRENBURG, *M. minima* MEYER, *M. obliqua* SCHEWIAKOFF, *M. sociabilis* MEYER, *M. socialis* (KENT) LEMM, *M. vestita* (STOKES) REYNOLDS, *M. vivipara* EHRENBURG.

II. Observations on *Monas vestita* (STOKES, 1885).

This study is based on specimens obtained from stale cultures of pond water collected near the University of Virginia. Except for the general absence of an attaching stalk, the organisms so closely resemble the form described by STOKES (1885) as *Physomonas vestita* that the two are considered to be identical. Reasons for transferring the species to the genus *Monas* are given in the discussion.

a) General morphology.

The organisms are small, ovate ($10-15\ \mu \times 7-10\ \mu$) and practically colorless. A principal flagellum, about twice the length of the body, arises from the anterior end; near its base is an accessory flagellum, which is 0.5 the body length. The body is enveloped by a covering of what appears to be solidified mucus. From this covering numerous slender threads radiate in all directions (Pl. 12 Fig. 1). The mucous envelope is from one to two microns thick, while the mucous threads are six to eight microns long. There is no mouth, but a mouth-vacuole is always formed in a definite region (Text-Fig. 3b). Numerous food vacuoles may be seen scattered through the cytoplasm. Solid waste products pass out through the surface near the posterior end (Text-Fig. 3c). A contractile vacuole is located near the mid-region of the body on the side opposite from the mouth-vacuole. Occasionally an additional vacuole may be seen near this, or on the opposite side. At the anterior end, on the side of the flagella opposite from the mouth-vacuole, there is a granular thickening in the cytoplasm, improperly called the "Mundstrick" (Pl. 12 Fig. 1t). The nucleus is located near the anterior end.

b) the nucleus.

The nucleus is of the vesicular type. It may be circular or slightly oval in optical section. The width is from 2.5 to 3 μ . The karyosome is from 1.5 to 2 μ . It is suspended from the nuclear membrane by means of spoke radii — about five being seen at one focus. Apparently it is not a compact mass, for the center is less dense (Pl. 12 Fig. 2). In the space between the karyosome and the nuclear membrane are numerous minute granules.

In fixed specimens the nucleus appears to be embedded in a stellate mass of denser cytoplasm, the anterior prong of the mass being specially modified to form the connection with the flagella. Stained preparations of dividing specimens were not observed, consequently nothing can be said of cytological details during division.

c) the flagella.

The two flagella arise from the cone of protoplasm which extends from the nuclear membrane to the anterior end of the body. They are of approximately the same diameter, though one is four or five times longer than the other. While swimming around, the

longer flagellum is held in front, the proximal half practically straight and the distal half curved towards the side where the mouth-vacuole will be formed. Throughout the distal two-thirds of its length it usually is rapidly oscillated in a plane perpendicular to the plane of its curvature, thus taking on the appearance of a spatulate structure¹). This movement of the principal flagellum is primarily for the purpose of procuring food, though it necessarily helps to propel the organism through the water. Movement of the short flagellum is undulatory in nature. It seems to be specially concerned with locomotion.

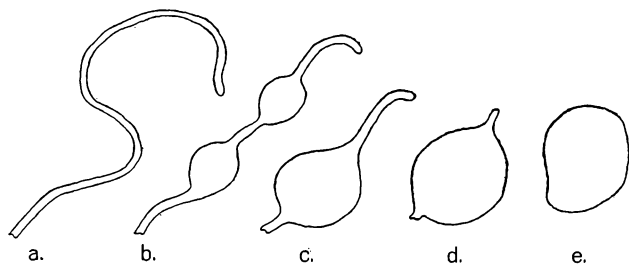


Fig. 1. Long flagellum came in contact with rays of *Actinophrys sol*. Apparently it was injured and became detached from the body, a. The shapes assumed by it during the next two minutes are shown by b after $\frac{1}{4}$ min., c after $\frac{1}{2}$ min., d after 1 min. and e after 2 minutes.

ch, following an injury. As shown by Text-Figs. 1 a, b, c, d, and e, a detached flagellum quickly assumes a spherical form and at no stage in this process is there anything to indicate the presence of an axial filament. A similar phenomenon may be seen just prior to division. As the long flagellum is resorbed its distal end becomes knobshaped (Text-Fig. 2 c). PIETSCHMANN (1929) shows a similar condition in the flagella of *Vahlkampfia tachypodia*. McCONNEL (1931) observed a knobbed condition in the developing flagella on the endodermal cells of *Hydra*. In *Monas vestita*, however, the knobbed appearance is never in evidence on developing flagella.

Within nine minutes from the time a flagellum is dropped a new one may be seen growing out from the base. It attains its full length and function within twenty minutes from this time. No observation was made of the loss of the short flagellum.

¹) For further information concerning flagellar movement in this genus reference is made to the works of METZNER (1920) and KRIJGSMAN (1925).

The flagella seem to be constructed like a tube. No indication of an axial filament has been observed. In several cases the long flagellum was seen to become detached.

d) division.

Under optimum conditions cell division takes place every four or five hours. Stained preparations were not obtained of organisms in this process, consequently observations are restricted to external features. Several interesting phenomena were seen which help to clarify the confusing statements of earlier investigators regarding the number of flagella.

Preparatory to division the accessory flagellum is resorbed. (Text-Fig. 2a). Shortly thereafter two new flagella grow out (Text-Fig. 2b). The two flagella which have arisen after the resorption of the short flagellum grow out until they attain the length of a long flagellum, while the original long flagellum is represented by a knobbed process (Text-Fig. 2d). As the old long flagellum disappears into the cytoplasm, two new short flagella arise from near its base (Text-Fig. 2e). At this stage it can be seen that the organism is beginning to divide, a long and a short flagellum moving apart with each zooid (Text-Fig. 2f). Ultimately the two daughter organisms are pointed in opposite directions and remain connected by only a thin strand of cytoplasm (Text-Fig. 2g). In time this breaks and they swim off as independent animals. The entire process of division takes place within twenty to thirty minutes.

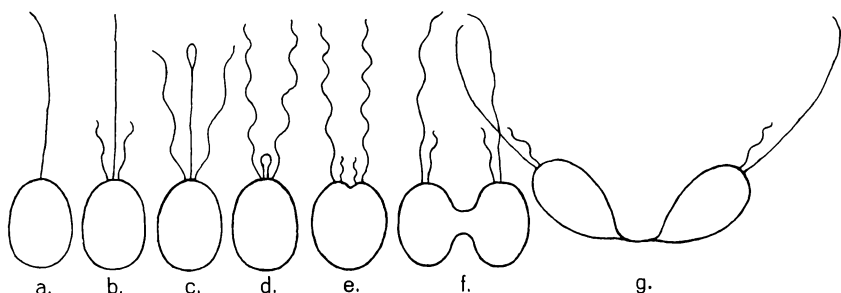


Fig. 2. a Short flagellum has been resorbed. b Two new flagella growing out. c Old long flagellum shows knobbed end as it is being resorbed. d Old long flagellum practically gone as new long flagella reach their full length. e Two new short flagella arise from base of old long flagellum while the cell begins to divide. f and g Further stages in division. Time represented from a to g is twenty minutes.

An interesting point in this connection is the fact that during division the flagella are resorbed at different times, two new long flagella arising after the disappearance of the old short flagellum, while from the base of the old long flagellum two new short flagella develop.

By referring to Pl. 12 Fig. 2 it will be seen that the two flagella arise from a common protoplasmic cone, the zygoblast. If we consider the position of the mouth-vacuole as ventral, the bases of the flagella are laterally disposed to each other. Apparently the plane of division is dorso-ventral. It seems that after the short flagellum has been resorbed a new flagellum grows out from the zygoplast on either side of the old long flagellum. Then with the resorption of the old long flagellum, the two new short flagella which arise from its base are mesial to the two new long flagella. These positions of the flagella are shown in Text-Figs. 2e, f, and g.

Attention should be called to the fact that the long flagellum retains a semi-rigid position most of the time while it is being resorbed. As the new long flagella grow out, however, they undulate similar to the usual movement of the short flagellum. It is only after they have attained their full length and the process of division has been practically completed that they assume the characteristic arcuate position.

During division the mucilaginous covering is lost. As the two daughter zoids separate it may be seen as a tangled mass scattered around them. In this condition one has no difficulty in recognizing that the radiating threads are of the same composition as the investing covering. Even before division is complete new mucilaginous threads begin to appear — and the mucous covering, thin at first, gradually becomes thicker.

e) feeding.

M. vestita feeds on minute plant and animal cells. Usually the organisms serving as food are less than one micron in diameter. Occasionally larger objects, such as diatoms, are ingested.

The rapid vibration of the primary flagellum creates a current in the water. If food particles come in contact with this flagellum it is quickly flexed in such way as to convey the particle towards the region of the mouth-vacuole, the flagellum itself generally touching the side of the body (Text-Fig. 3a). In some cases the food may strike against the body causing the necessary stimulus. In response to this stimulus a forward projecting food cup is formed. Into this the food passes, being drawn in by suction — and in some cases, apparently, the flagellum aids by pushing (Text-Fig. 3b). Observations have been made in which the food particles would escape from the curvature of the flagellum after the latter had

given the thigmotactic stimulus. In these cases the food cup would be formed, though no food was present. The short flagellum is usually pushed towards the center and is relatively inert during the process of food ingestion.

f) parasitized individuals.

A number of these flagellates were parasitized by a small organism (presumably one of the Chytridiaceae), see Pl.-Fig. 3 b, p. PERTY (1852) and STEIN (1878) observed the same phenomenon. STEIN considered it to be a sexual process. On page 98 he says: „Ich glaube daher, daß hier ein Conjugationsact zweier Individuen vorliegt, der mit der vollständigen Verschmelzung beider zu

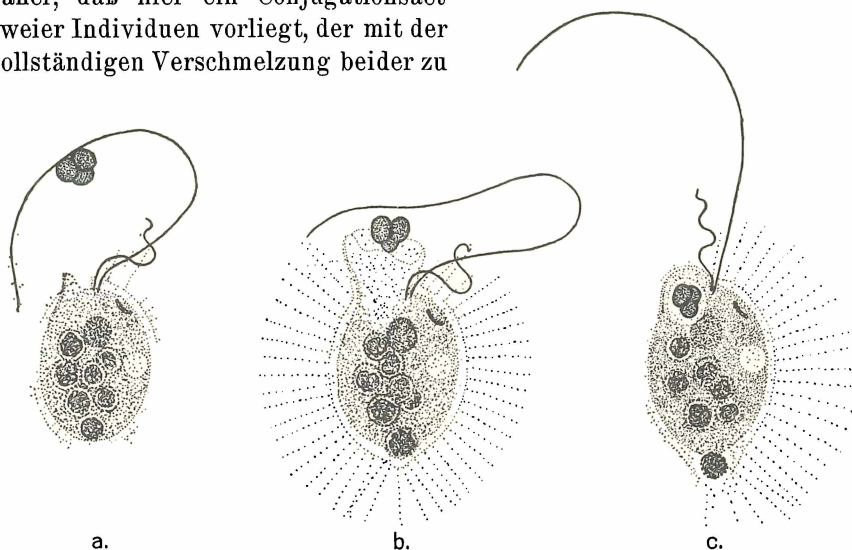


Fig. 3. a Food brought towards mouth-region by long flagellum the tip of which strikes side of body, thereby giving initial stimulus for formation of food cup. b Food being sucked into cup after having been brought nearer by greater flexion of the long flagellum. c Process of ingestion completed, long flagellum has resumed its normal position. At posterior end dejecta is passing from the body.

einem Thiere, der geschlechtlichen Generation, endigt und werde dies im speciellen Theile weiter zn begründen versuchen." In part, this is responsible for the general statement, made sometimes, that sexual reproduction occurs through the copulation of individuals.

A prolonged study of parasitized forms was not made; therefore, a report of the effects cannot be given.

Discussion.

MÜLLER should be given credit for the genus name *Monas*, rather than EHRENBURG. Although this characterization of the monads as punctiform organisms is very indefinite; yet, it isn't, as inappropriate as EHRENBURG's statement regarding their unvarying form. Credit for the family name *Monadidae* is properly given to EHRENBURG.

The most accurate description of the genus *Monas* given by the pioneers in this field is that of DUJARDIN (1841). Aside from the omission of the secondary flagellum (which had not been observed) his definition of the genus *Monas* is approximately adequate for the present time. It is as follows: „An. nus, de forme arrondie ou oblongue; de forme variable, sans expansions, et avec un seul filament flagelliforme, — Mouvement un peu vacillant.” STEIN's (1878) emendation of the genus differs from DUJARDIN's definition primarily in that he mentions one or two accessory flagella. As shown in part II of this paper, one is the normal number of accessory flagella in *Monas vestitia*; if two are present it is because cell division has been initiated. The same condition was found to be true for *M. guttula*. This probably holds for all of the species.

Owing to the extreme variability in form that may be observed in a single individual, shape is not considered to be an important criterion for making specific distinctions; neither should too much emphasis be placed on size. In pure cultures of *M. guttula* one may observe at one time both free and attached individuals, while among them may be found spherical, pyriform, or elongate specimens. Some of the individuals thus observed were practically identical in shape and size with *Sterromonas formicina* KENT. This constitutes the basis for considering KENT's flagellate to be a synonym for *M. guttula* EHRENBURG.

Attention has been called to the fact that STEIN, KENT and others considered *Monas guttula* EHRENBURG and *Spumella vulgaris* CIENK to be identical. Study of the subject does not reveal specific differences to me. Since *M. guttula* has priority, *M. vulgaris* should be relegated to the position of a synonym.

It is not considered necessary to give further reasons for not accepting *M. micropora* as a valid species.

M. obliqua is tentatively retained, though it is probable that a description based on a more careful study of *M. elongata* would have made it unnecessary to create this species.

Physomonas vestita STOKES is transferred to the genus *Monas*. Its principal difference from other members of that genus lies in the fact that it is invested with a mucilaginous covering from which fine threads radiate. This mucilaginous material appears to be of the same composition as the pedicle by which many monads, including *M. vestita*, are attached. If this be true, then this species is more abundantly supplied with a substance common to most representatives of the genus. Evidence of this is indicated by the fact that some specimens show much thinner coverings and a smaller number of radiating threads than one generally encounters.

The primary difference between *Monas vestita* and the organism on which the second part of this study is based is that STOKES described the former as being attached. Most of the specimens observed in this work were free. A few, however, were attached and agreed in virtually every detail with STOKES' description of the flagellate which he called *Physomonas vestita*. In view of the fact that further observations have not been made on the flagellate described by STOKES, it seems best to consider that the two organisms belong to the same species and that most of the specimens observed by me were free, where as most of the specimens observed by STOKES were attached.

PROWAZEK (1903) states: „Bei einer Varietät der *Monas guttula* EHRLH, besitzt der Zygoplast die Form eines sehr hohen, schmalen Stengelglases und besteht anscheinend aus einem dunkleren, homogenen Plasma und wird durch den Rhizoplast einer basalkornführenden Geißel durchbohrt". Later in the same paper he says: „Bei der *Monas vivipara* . . . besitzt der Zygoplast eine mehr bisquitförmige Gestalt ohne weitere, feinere Details erkennen zu lassen". In *M. vestita* the condition is more like that in *M. guttula*. The zygoplast extends from the nuclear membrane to near the anterior cell-surface as a cone-shaped or wedge-shaped structure. At its distal end is a chromatinic body which presumably is the homologue of the blepharoplast. This, however, is not connected with the nucleus by a rhizoplast as PROWAZEK described for *M. guttula*. In stained preparations the appearance of the neuro-motor complex is similar to that pictured in *Vahlkampfia tachypodia* by PIETSCHMANN (1929), except that the zygoelastic cone is extranuclear instead of being a prolongation of the anterior rim of the nucleus.

The absence of an axial filament lends support to METZNER'S (1920) statement regarding the small number of cases in which there is definite evidence that flagellary movement is accomplished by the

antoganistic workings of a contractile plasma covering and a central elastic thread. Attention has been called to the rapidity with which the long flagellum oscillates. It seems probable that this type of motion, the peculiar resorption of old flagella, and the rapid growth of new flagella are conditioned by the large zygoplast to which the flagella are attached. Perhaps a study of all the species would show these to be generic characteristics.

Summary.

1. Thirteen species of the genus *Monas* are recognized as valid.
 2. *Monas vulgaris* is a synonym for *M. guttula*.
 3. *Sterromonas formicina* KENT is a synonym for *M. guttula*, thus the genus *Sterromonas* KENT does not contain a species.
 4. *Physomonas vestita* STOKES is transferred to the genus *Monas*, thus leaving the genus *Physomonas* KENT without a species.
 5. Prior to division in *M. vestita* the short flagellum is resorbed, following which two new long flagella develop; then the old long flagellum is resorbed and from its base two new short flagella arise.
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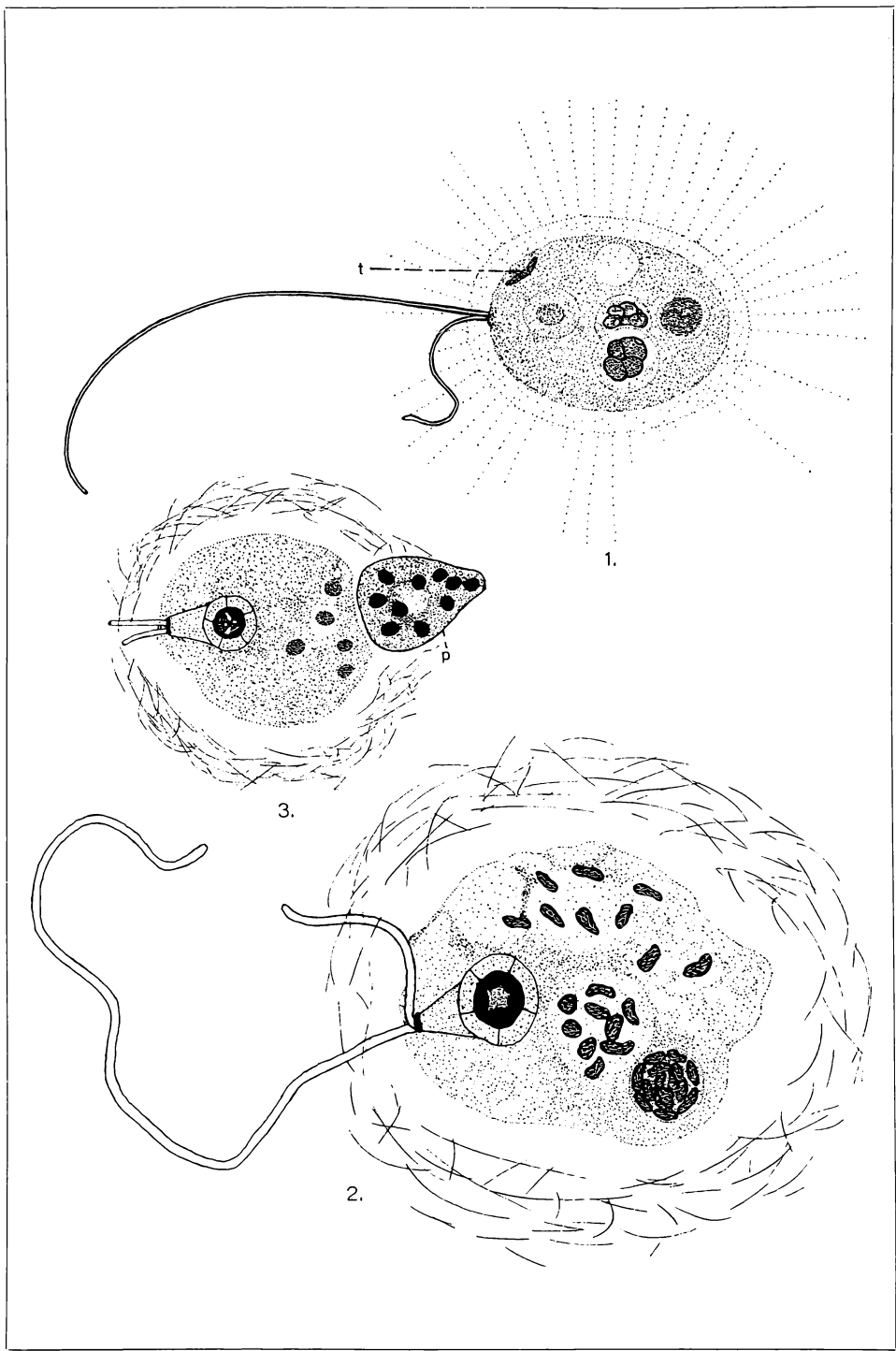
Explanation of Plate.

Plate 12.

Fig. 1. Characteristic appearance of living *Monas vestita*. t Region of denser cytoplasm — the "Mundstrich". \times 2700.

Fig. 2. Specimen stained with iron-hematoxylin; showing nucleus, zygoplasmic cone, food vacuoles, scattered food particles and mucous investment. \times 4200.

Fig. 3. Stained preparation of parasitized individual. \times 2700.



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