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Bohuslav Fott:

Taxonomy of *Mallomonas* based on electron micrographs of scales

The first electron micrograph of a scale of *Mallomonas* was taken by myself and Rozsíval in 1951 and published a few years later (Fott 1955). In that paper I pointed out that the electron microscope reveals a wealth of markings on these scales and expressed the opinion that this submicroscopical structure is sufficiently characteristic for each species of *Mallomonas* to permit, as in *Synura*, reliable determination at the species level.

The idea that the shape and structure of the silicified scales of *Mallomonas* are of great taxonomic importance was originally put forward by Iwanoff (1899). He made drawings of *Mallomonas* scales as seen in the light microscope, but at this time only three species of *Mallomonas* were known. Unfortunately, many of the subsequent workers did not follow Iwanoff's suggestion and their diagnoses of *Mallomonas* species, based largely on cell-shape, fail to give any details concerning the size and structure of scales. A survey of all species described up to 1940 is given in Huber-Pestalozzi's Phytoplankton des Süsswassers (1941). He mentions 56 species of *Mallomonas*, but the structure of the scales, so far as it can be discerned in the light microscope, was known in only 17 of these. It is very difficult to determine the precise structure of the surface of a scale by light microscopy and no great specific differences are discernible, even when using high magnifications. It is usually only the presence or absence of a V-shaped structure or large pores which can be demonstrated, other details of scale-structure remaining unknown. Huber-Pestalozzi's comprehensive work, based on the morphology of cell, scales and bristles as seen in the light microscope, fails to delimit many of the species and his key permits only a few species to be reliably determined.

When I published my first electron micrographs of *Mallomonas* in 1955, I thought that, in the future, the taxonomy of this genus would be worked out without difficulty, as it has been for *Synura*, by reference to the specific scale-patterns revealed by electron microscopy. During the last six years many electron micrographs of scales have been published (Asmund, Fott et Ludvík, Harris et Bradley, Takahashi) and a new problem has arisen: how to decide which is the correct specific name to go with a particular electron micrograph of a *Mallomonas* scale. This difficulty, as already mentioned, is due to the fact that only a small number of species can be reliably determined by means of the key given by Huber-Pestalozzi (1941). Electron micrographs of *Mallomonas* scales are taxonomically useful only in those cases where it is possible to determine the species to which a particular scale belongs. The scale-patterns seen in the electron microscope must not be in contradiction with the structure of the scale described by means of light microscopy in the original diagnosis. The aim of future investigations in the taxonomy of *Mallo-*

monas is to discover the structure of scales by electron microscopy and thus to define the species "electron microscopically", bearing in mind in this procedure that it is necessary to respect existing taxa and the International Code of Botanical Nomenclature.

Results of electron microscopical investigations can help to solve the taxonomy of *Mallomonas* in two ways. Firstly, where the scale-structure justifies it, we can safely combine and make synonymous those species in which the external appearance shows such a degree of diversity that they have been described by various authors as different species. For example, the electron micrographs of *Mallomonas coronifera* MATVIENKO and *M. schwemmlei* GLENK show the scales to be quite identical in structure, although the external morphology of these flagellates may vary slightly. These species must be made synonymous, in accordance with the International Code of Nomenclature. Conversely, differences in the structure of scales enables one to separate species in which external morphology is identical or nearly so. For instance, *M. doignonii* BOURRELLY, which was thought (HARRIS & BRADLEY 1957) to be identical with *M. coronifera*, proved to be an independent species with its own individual scale-pattern, and there are other such cases where further investigation of the submicroscopical structure of scales will lead to new descriptions of species. No description of a species of *Mallomonas* is now complete unless it includes an electron micrograph of the scales.

Morphology of silicified scales and bristles in *Mallomonas*

IWANOFF (1899) was the first to show that scale-structure in *Mallomonas* might be of importance in distinguishing species and he made drawings of V-shaped structures on scales and of a bristle with a helmet-shaped tip. At this time only three species were known.

CONRAD (1933) used the shape of the cell, the presence or absence of bristle (and their position) and the structure of scales as the taxonomic criteria. On the basis of the outline of the scale he divided the genus into several groups: Triangulares, Quadratae, Ellipticae, Discoidae. A modified form of this classification was used by HUBER-PESTALOZZI (1941) and BOURRELLY (1957).

HARRIS and BRADLEY (1957, 1960) suggested a system of grouping species based on the structure of their scales as seen in the electron microscope and they introduced some terms which have proved to be very useful in the descriptive morphology of scales and scale-location on the cell-body of *Mallomonas*. The position of a scale in the cell armour is described by the terms "anterior" and "posterior" for scales lying at the ends of the cell, while the others are referred to as "body scales". The end of the scale which overlaps its neighbour is called the "distal" end, and this is where the bristle is attached in bristle-bearing scales. The "proximal" end of the scale is that which is overlapped by its neighbour.

The scale itself bears various structures, some of which can be seen in the light microscope, especially with phase contrast, but their precise configuration is discernible only in the electron microscope. The most striking features, when present, are the "V-rib" and the "dome", a cicatrix-like cavity from which the bristle emerges. That part of the scale within the arms of the V-rib is the "shield", the narrow outer edge is the "flange". HARRIS (1953) calls such scales "tripartite scales", since they are composed of three parts: the dome, the shield and the flange. In reality, these parts are not distinct entities, capable of separation, they are only the delimitations of the various areas of a single entire scale.

The rib is a strong V-shaped ridge, either simple and smooth or strengthened by short transverse struts; in some cases, it is roofed at the proximal end by a hood. In tripartite scales, both arms of the V-rib are bent towards the dome and attached to its edge. In Torquatae-scales the rib is rhomboid, being composed of two V-shaped ridges, one at each end of the scale, the arms of which

join together in the middle of the scale. The scales of the Planae and Quadratae groups exhibit no ridges and no dome.

The shield can be smooth or bear transverse ridges which lie parallel to one another and more or less connect the arms of the V-rib. In other cases the shield has a reticulate structure of hexagonal meshes. The dome is the convex distal part of the scale, under which the foot of the bristle is attached. The way in which the bristle is affixed to the dome on the inner side of the scale was

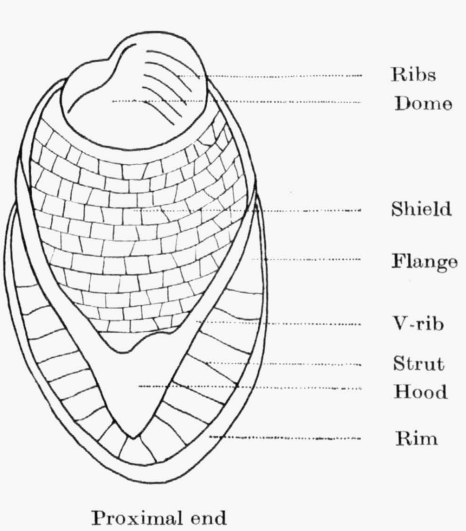

Fig. 1. — Diagram of a tripartite scale of *Mallomonas* as seen in the electron microscope

demonstrated by BOURRELLY (1957) by means of direct observation in the light microscope and confirmed electron microscopically by HARRIS and BRADLEY (1957) using the replica technique on *M. leboimei*.

Scales of *Mallomonas* are perforated by small pores, arranged more or less regularly; there are no "opaque" scales (that is, without pores) in the genus.

The bristles show more details in the electron microscope than can be seen in the light microscope, though even IWANOFF (1899) noticed that the bristles are hollow, a fact which has been confirmed by electron micrographs. Usually the bristles are slightly bent, flattened and unilaterally serrated at the distal end, though in *M. leboimei* the bristle exhibits three edges each of which bears different, distinctive teeth. In the light microscope some bristles seem to be smooth but the electron microscope reveals minute teeth at the distal end of the bristle. In general, bristle serration shows great variations in size and number of the teeth. Bristles of some species are provided with a helmet-shaped tip (Fig. 4). At the proximal end, the bristle is usually abruptly curved into a "foot", by means of which the bristle is inserted under the dome and attached to the body of the scale.

The scales from the posterior end of the body (rear scales) of some species may bear spines. These are not appendages of the scale, but outgrowths of the scale margin. The spines may be quite short like teeth, but in mature stages in some species they become longer and look like the bristles.

Taxonomy and infraspecific variability of *Mallomonas acaroides* PERTY emend. IWANOFF

The description of this species by PERTY (1862, p. 171) is very simple and no details about scales and bristles are given (Fig. 2). The species is no doubt identical with *Mallomonas Plösslii* PERTY, as the author himself says (l.c.p. 171) "*Mallomonas Plösslii* formerly *Mallomonas acaroides*". PERTY did not observe the scales, he described only bristles. Various workers subsequently recorded and drew ovoid *Mallomonas* species measuring 18—30 μ, covered with many bristles (FRESENIUS 1858, STEIN 1878, KENT 1882, ZACHARIAS 1893, etc.) which they named either *M. acaroides* PERTY or *M. Plösslii* PERTY, but only KLEBS (1893) discerned small ovoid scales and he failed to give any notes on their structure (Fig. 3*d*—*g*). If we make a survey of the numerous records and drawings of these older authors, it is seen to be doubtful whether all these pictures, drawn as ovoid cells with numerous bristles, belong to *M. acaroides*.

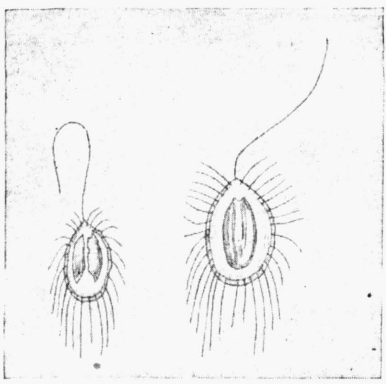

Fig. 2. — Iconotype of *Mallomonas acaroides* PERTY. — Reproduced from CONRAD 1927 after PERTY 1851.

IWANOFF (1899) was the first to fix the main characteristics of the species in terms of scale structure and the shape of bristles, and distinguished, using these features, the other species of *Mallomonas* known at that time. His diagnosis is short and quite clear (l.c.p. 249):

"Der ovale Körper ist 20—26 μ long und 7—12 μ breit. Der Panzer besteht aus ovalen Schuppen von 5,5 μ Länge mit 2 Linien, die zur Bildung eines Winkels in einiger Entfernung vom Rande der Schuppe zusammentreffen. Die Nadel ist ganz am Rande befestigt (Taf. A, Fig. 1). Die Nadeln (getrocknet) sind dünn, durchsichtig und vom Grunde an und ihrer ganzen Länge nach hinten zurückgebogen. Sie sind glatt oder mit 2 Zacken (Taf. A, Fig. 3) am freien Ende und bis 24 μ lang. Meist sitzen sie dicht auf der ganzen Oberfläche des Körpers. Kommt in Teichen und Sümpfen vor."

IWANOFF's drawings (Fig. 3*a*, *b*, *c*) show the details that are typical for this species: ovoid scales with two ribs forming a V-structure and bristles provided with two teeth at their tips. Only IWANOFF's description has defined *M. acaroides* PERTY distinctly and this is a true type-drawing of the species. As he added the important details on scales the species should be called *M. acaroides* PERTY emend. IWANOFF.

However, most subsequent authors failed to make use of IWANOFF's diagnosis and did not respect the typical structure of scales and the peculiar ending of bristles. PASCHER (1910, p. 33; 1913, p. 39) adopted the description of IWANOFF and mentioned the V-structure and two teeth on the bristle, but judging from his figure, it is not certain that he has, in fact, drawn *M. acaroides*. CONRAD (1927) tried to elucidate the confused taxonomy of *M. acaroides* and proved that the name *M. acaroides* PERTY is valid; he also reproduced IWANOFF's drawing of scales and bristles (see my fig. 3*a*, *b*, *c*). KRIEGER (1932, p. 293) based his description on the interpretation of CONRAD, but added his own drawing which differs from the original drawing of IWANOFF in a very important

detail: the V-structure on the scales is not formed of two ribs, but of two convergent rows of dots. In view of the difficulty of drawing the inconspicuous structure of the scales as seen in the light microscope, it is possible that KRIEGER (1932) expressed in these dotted lines the ribs of the V-structure, since in his description there is no mention that the rib might be interrupted and composed of dots. CONRAD (1933) included this interpretation in his monograph as a fact, giving the drawing of scales with two convergent rows of dots and emphasizing these details in his diagnosis: "un dessin en V, formé de gros points" (l.c.p. 40). Unfortunately this interpretation of the V-rib was taken over in the monographs at present in use for species determination (HUBER-PESTALLOZZI 1942, MATVIENKO 1954), althought their drawings of the V-rib are in contradiction with the first drawing of IWANOFF. Only BOURRELLY (1957, pl. VI, fig. 16) figures the V-rib on scales of *M. acaroides* in the same way as IWANOFF (1899).

This fact caused a further complication in the infraspecific taxonomy of the species, as subsequent authors (HARRIS & BRADLEY 1960, ASMUND 1959) held this variety with dotted V-rib (which they had not seen themselves,

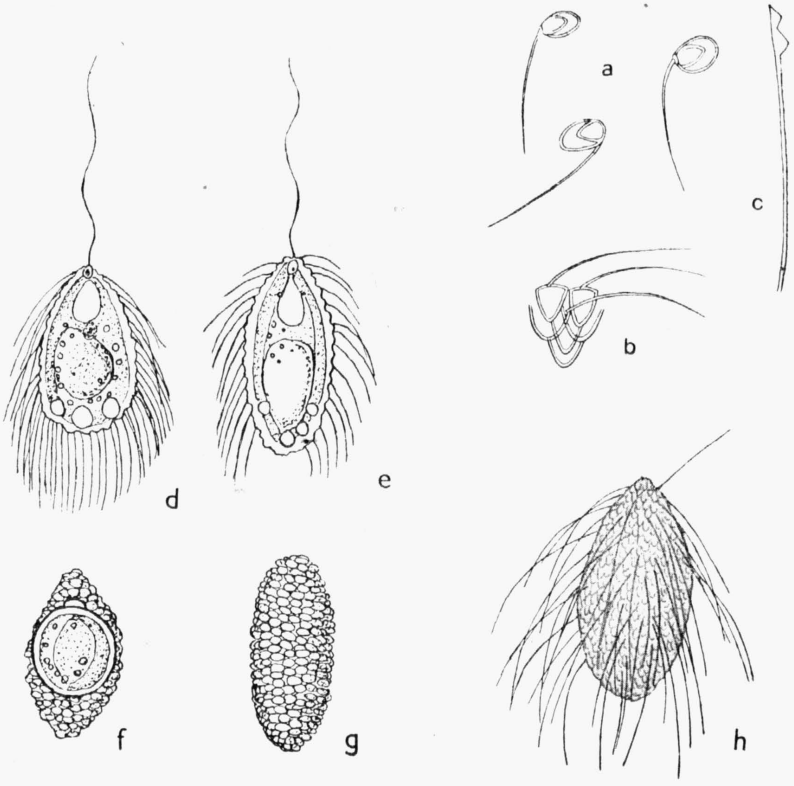

Fig. 3. — Some drawings of *Mallomonas acaroides* PERTY, reproduced from CONRAD 1927 after older authors. — *a*, *b* scales and *c* bristle after IWANOFF 1899. These figures present in fact a type of the species, as the main characteristics of it (the V-rib and the helmet-shaped bristle) are clearly illustrated. — *d*—*g* after KLEBS 1893. Here for the first time the scales and a cyst of *Mallomonas* are demonstrated. — *h* after PASCHER 1913.

of course!) to be a type variety (var. *acaroides*) in describing new varieties. Their mistakes is that the basic type for distinguishing new varieties is not var. *acaroides* sensu CONRAD (with dotted V-rib), but var. *acaroides* sensu IWANOFF, as shown above.

Personally, I am persuaded that only IWANOFF's drawing of the V-rib is correct, whilst KRIEGER's and CONRAD's V-structure of dotted lines is a misleading interpretation of the same feature. It is well known in phycology that the same structure can be drawn in different ways by various workers according to observing and drawing ability, according to the magnification and quality of the microscope used, and so on. In fact, the ribs of the V-structure are not smooth, but crossed with some transverse struts, figured in the light microscope by BOURRELLY (1957, pl. VI, fig. 14) and photographed by me (pl. I : *e*). Presumably, KRIEGER and CONRAD have drawn dotted lines when observing these struts which are not visible as such, but as separate bodies, in the light microscope. Nowadays, many electron micrographs of the V-structure are studied and in no case have the dotted lines been detected. The dots seen on scales of *M. allorgei* (DEFLANDRE) CONRAD and *M. lychenensis* CONRAD are, in fact, pits or large depressions (HARRIS & BRADLEY 1960). For these reasons I have decided that the dotted lines of CONRAD (1933, fig. 30) and KRIEGER (1932, fig. 35c) are an incorrect drawing of the same structure as that drawn by IWANOFF (1899).

When we compare the numerous species of *Mallomonas* listed in HUBER-PESTALOZZI and the drawings of additional species described by BOURRELLY and subsequent authors, it is clear that the V-structure of scales and the teethed bristles as seen in the light microscope are not sufficient to delimit the various *Mallomonas* species exactly. There are some species which look very similiar to *M. acaroides* as described by IWANOFF and it is not possible to differentiate them on the basis of their external morphology. In this situation there is only one way to separate them: by using the scale-pattern as seen in the electron microscope as a taxonomic criterion.

Today we have electron micrographs of *Mallomonas*-scales taken by three workers from different parts of Europe, which all show an identical patterning of the scale which agrees with IWANOFF's drawing. The markings on scales reproduced by ASMUND (1949, Fig. 28, this paper tab. II : *b*), by HARRIS & BRADLEY (1960, Pl. 1, fig. 7, this paper tab. II : *a*) and by me (FOTT 1955, tab. V, this paper tab. II : *d*) are absolutely identical. They prove the validity of the statement that the pattern of the *Mallomonas* scale is characteristic for each species. Among the 35 micrographs of *Mallomonas* scales taken by various workers up to the present time, there is none showing a pattern which could be mistaken for that of *M. acaroides*, as figured in this paper (Tab. I, - III).

The scale of *M. acaroides* is a so-called Tripartite scale, since it is composed of three distinct areas: the shield, the dome and the flange. The shield is separated from the flange by the V-rib. The whole body of the scale is perforated by numerous pores disposed regularly, but forming no geometrical system. The shield is rhombic in shape, bordered in the proximal part by the ribs of the V-structure, in the distal part by prolonged extremities of both arms of the V-structure; these bent arms lead to the dome. This is in fact a rhombic frame, the proximal part of which is stouter and is seen as the mentioned V-structure. At the proximal part, where the two arms join together, there is a hood forming an asymmetrical roof. The flange is quite broad, having

an upwardly folded margin. On both sides of the V-rib there are short transverse struts. Some of these lead from the rib to the folded edge of the scale, the others, being too short, do not reach it and disappear in the middle of the flange. Similar short struts project towards the area of the shield. The dome is an elliptical convex projection, the long axis of which lies transversaly to the long axis of the scale. The bristle is inserted below it in an opening showing an S-shaped structure.

In the preceding description of the scale of *M. acaroides* I have taken into consideration only the species itself and not the varieties. The varieties var. *epilis* PERTY 1852, var. *grandis* PASCHER 1913, var. *lacustris* LEMMERMANN 1910 and var. *moskovensis* (WERMEL) KRIEGER 1932 are mostly imperfectly described and without information about the scale structure. They must be abolished, as it is not possible to recognise them. Whether *M. acaroides* PERTY f. *tatrica* WOLOSZYŃSKA 1939 really belongs to this species is very doubtful. The species does exhibit helmet-shaped ends to the bristles, but the pattern on the scales is quite different. This taxon must therefore be excluded from the species *M. acaroides*.

BOURRELLY (1957) described var. *denticulata* and var. *dimorpha* as characterised by the serrated spines or by their dimorphism. Both taxa seem to be well substantiated, but in so far as the submicroscopical structure of scales is not known there is no certainty about their taxonomic position.

ASMUND (1959) defined var. *striatula* by means of electron micrographs of scales and bristles. Whereas the scales show the same pattern as scales of species from England (HARRIS et BRADLEY 1960) or Czechoslovakia (FOTT 1955, this paper tab. II*a*, *d*), the bristles reveal some features which might substantiate a new variety.

HARRIS et BRADLEY (1960) described var. *galeata* which differs from the type (var. *acaroides*) in having the V-rib without fine dots and in all its bristles possessing helmet-shaped tips (l.c.p. 765). Unfortunately the authors did not regard the important fact that the "type" of *M. acaroides* PERTY is not *M. acaroides* sensu CONRAD 1933, but *M. acaroides* PERTY emend. IWANOFF 1899, which is the oldest type based on the structure of scales and bristles. In IWANOFF's drawing the V-rib is not dotted, but has the same appearance as in the drawing of HARRIS et BRADLEY (l.c.p. 756, fig. 10).

For this reason I am persuaded that var. *galeata* HARRIS et BRADLEY is in fact the "type variety" and according to the International Codes of Nomenclature should be called *M. acaroides* PERTY emend. IWANOFF var. *acaroides*. In transferring HARRIS' and BRADLEY's variety to the status of type variety, var. *acaroides*, we have obtained a perfect and complete description, based on the observations in the light microscope, agreeing with those in the electron microscope. This description and the relevant figures are in full conformity with the fundamental emendation of IWANOFF. The real varieties of *M. acaroides* will differ from this type variety, var. *acaroides*, largely by the morphology of the bristles. The basic submicroscopical structure of the scales remains in all varieties the same (see tab. II).

Mallomonas acaroides var. *echinospora* (NYGAARD) FOTT comb. nova is a further variety that can be established according to the principles I have just outlined. Electron micrographs of scales show that the main pattern is the same as in var. *acaroides*, except that the struts on the shield and on the flange are broader and coarser with more undulated sides. In contrast to var.

acaroides the bristles are unilaterally serrated with no helmet-shaped tips. According to NYGAARD (1949) the variety is distinct in having verrucose cysts ("cystis globosis, spinis tenuibus tectis", l.c.p. 122). In fact other varieties (e. g. var. *acaroides* = var. *galeata* HARRIS et BRADLEY) also have verrucose cysts, so that this characteristic does not seem to be important.

Fig. 4. — Bristles of *Mallomonas acaroides* as seen in the electron microscope. — *a* helmet-shaped bristle tip and a bristle transition between helmet bristle and serrated bristle of *M. acaroides* var. *striatula* ASMUND. — *b*, *c* serrated bristles from the same variety. — *d* body bristle and *e* apical bristle of *M. acaroides* var. *echinospora* (NYGAARD) FOTT. — After ASMUND 1949.

The variety var. *echinospora* NYGAARD was described originally as a variety of *Mallomonas pediculus* TEILING. ASMUND (1959) who studied the species in the electron microscope is not sure where to place it. She writes (l.c.p. 37): "All the divergences of *M. pediculus* from *M. acaroides* may be differences of degree and not of kind. It must therefore remain a matter of opinion whether *M. pediculus* is a distinct species or should be classified as a variety of *M. acaroides*". For this reason I think my transfer of this taxon to the species *M. acaroides* as a var. *echinospora* is entirely justified.

Having determined the submicroscopical structure of scales of *M. acaroides* as shown by electron micrographs, it is possible to put in this species taxa described under other names. Thus the species yielding the first electron migrograph of a *Mallomonas* scale, determined by me (FOTT 1955) as *M. tonsurata* TEILING, is in fact *M. acaroides*, as its submicroscopical scale-pattern is identical with that of this species. The taxon I examined differs from var. *acaroides* by the lack of a helmet-shaped tip to the bristles and by possessing bristles only on the anterior part of the body. I therefore suggest transferring *M. tonsurata* TEILING var. *alpina* (PASCHER et RUTTNER) KRIEGER sensu FOTT 1955 to the species *M. acaroides* PERTY emend. IWANOFF as a new variety, var. *inermis*.

On the other hand, some *Mallomonas* species referred to *M. acaroides* have to be excluded from this species. Thus *M. acaroides* PERTY var. *crassisquama* ASMUND 1959 exhibits a different pattern on its scales to that of var. *acaroides*. The scale is, like that of *M. acaroides*, tripartite, but the shield bears a peculiar network of angular meshes. I hold this feature and characteristic appearance of the entire scale to be a difference at the specific level and think, therefore, that this variety should be changed to an independent species, *M. crassisquama* (ASMUND) FOTT comb. nova. The species has a cosmopolitan occurrence, being found in Denmark, Alaska and Czechoslovakia.

Mallomonas acaroides PERTY emend. IWANOFF

Tab. I—III

C e l l s ovoid or ellipsoid, broadly rounded at rear. Protoplast with 1—2 chromatophores and with many contractile vacuoles (up to 7). Flagellum as long as the body. Dimensions of the body: 10—30 μ × 7—18 μ.

S c a l e s elliptic, tripartite, lying across the body in oblique series, measuring 4—7 μ × 3—4 μ, bearing a distinct V-rib visible in the light microscope. In the electron microscope: dome elliptical, smooth, with an S-structure; V-rib stout, with an asymmetrical hood; shield smooth, structure-less; both arms of the V-structure and the rim of the flange connected by fine struts, short struts also passing to the shield; whole scale finely perforated by many pores.

B r i s t l e s slightly bent, more or less (sometimes inconspicuously) serrated, in some varieties helmet-shaped at the end, up to 35 μ long, hinged to scales over the whole body or lacking in the posterior part of it.

O c c u r r e n c e. In plankton of ponds and lakes, probably wide-spread.

V a r i a b i l i t y. There are now four varieties of *M. acaroides*, the scales of which show the same submicroscopical structure. They can be determined according to the following key:

1a. Bristles covering the whole body
  2a. Bristles of one kind only
    3a. Bristles with helmet-tip . . . . . var. *acaroides*
    3b. Bristles without helmet-tip, serrated . . . . . var. *echinospora*
  2b. Bristles of two kinds, with and without helmet-tip . . . . . var. *striatula*
1b. Bristles covering only the anterior part of the body . . . . . var. *inermis*

a) var. ***acaroides*** Tab. I, II: *a*

Mallomonas acaroides PERTY 1851 emend. IWANOFF 1899 var. *acaroides*

Synonyma:

Mallomonas acaroides PERTY 1851, p. 171, tab. 14: 19A, non B, C; FRÉSENIUS 1858, p. 217, tab. 10: 39—41; STEIN 1878, tab. 14: 4, non fig. 3, 5; KLEBS 1893, p. 417, tab. 13: 12ad (sub *Mallomonas Plösslii* PERTY); ZACHARIAS 1893, p. 16—17, fig. 13ab (sub *M. acaroides* ZACHARIAS); IWANOFF 1899, p. 249, tab. A, fig. 1—3; LEMMERMANN 1899, p. 109 (*M. acaroides* var. *lacustris* LEMMERMANN); PASCHER 1910, p. 33, tab. 2 : 9, 20; PASCHER 1913, p. 39, fig. 64 (incl. *M. acaroides* var. *grandis* PASCHER); PLAYFAIR 1915, p. 106, tab. 2 : 1—2; CONRAD 1927, p. 486—493, fig. 32—36; KRIEGER 1932 p. 292—293, fig. 35 [incl. var. *moskovensis* (WERMEL) KRIEGER]; CONRAD 1933, p. 39—41, fig. 29—30; HUBER-PESTALOZZI 1941, p. 106—107, tab. 24: 138; MATVIENKO 1954, p. 95, fig. 10—13; BOURRELLY 1957, p. 196, tab. 6: 12—15, fig. G5; PRESCOTT 1951, p. 371, tab. 96 : 22.

Cells ovoid, with closely set bristles over the entire surface. Scales large (4—7 μ × 3—4 μ), easily visible in the living cell; for the submicroscopical structure see tab. I: *d* and II: *a*. Dome prominent, pitted, shield smooth, flange sparsely ribbed. Bristles of one kind only, slightly bent, all with helmet-shaped tip, up to 35 μ long. Cysts spherical, scrobiculate, 18—22 μ in diameter.

Occurrence. Wide-spread, but not common. Electron microscopically-controlled records from England (Berkshire) by HARRIS et BRADLEY 1960, Czechoslovakia (in a pond in Bohemia) in this paper (tab. I). Reliable records from France and Sweden by BOURRELLY (1957).

Note. The variety can be recognised in the light microscope by means of the tripartite scale with V-rib and the helmet-shaped tip to the bristles. As helmed-tipped bristles are found in other *Mallomonas* species too, electron micrographs of scales are essential for correct determination. The electron micrograph by HARRIS et BRADLEY 1960, Pl. 1, fig. 7 (in this paper tab. II: *a*) can be used as a type for comparison.

b) var. ***echinospora*** (NYGAARD) FOTT comb. nova Tab. II: b

Mallomonas acaroides PERTY emend. IWANOFF var. *echinospora* (NYGAARD) FOTT.

Synonymum:

Mallomonas pediculus TEILING var. *echinospora* NYGAARD 1949, p. 122—124, Fig. 66 (basonym). ASMUND 1959, p. 35—38, fig. 31—33.

Cells ovoid, 11—30 μ in length, 6—18 μ in breadth, with bristles over all the surface. Scales oval (4—8 μ × 3.5—5.5 μ), electron microscopically similiar to var. *acaroides*, except that the V-rib and transverse struts are a little broader and coarser. Bristles of one kind only, curved, coarsely serrated unilaterally. Cysts verrucose, 14—18 μ in diameter.

Occurrence. Lakes in Denmark, in spring and autumn (NYGAARD 1949, ASMUND 1959)

Note. I transferred this variety from the species *M. pediculus* TEILING to the species *M. acaroides* PERTY, as the submicroscopical pattern of the scale is the same (compare tab. I : *d* and tab. II : *b*). The variety *echinospora* differs from var. *acaroides* in the morphology of bristles which are unilaterally serrated along the whole length and sharply pointed at the tip, without the helmet-shape. The cysts are strikingly verrucose, but only in the adult state.

c) var. ***striatula*** ASMUND Tab. II: c

Mallomonas acaroides PERTY var. *striatula* ASMUND 1959, p. 28—32, fig. 27—29.

Cells ovoid, rounded at the rear, about 20 μ in length and 10 μ in breadth. Scales oval (5.5—7 μ × 3.5—4 μ), tripartite, submicroscopical structure the same as in var. *acaroides*. Cysts spherical, verrucose, 16—20 μ in diameter. Bristles of two kinds, apical bristles shorter and broader than the body bristles. Some bristles with helmet-shaped tips, the others unilaterally serrated.

Occurrence. Denmark in Borupgaard Dam in a plankton-community (ASMUND 1959).

Note. This variety is characterised by the dimorphism of the bristles. The helmet-tipped bristle is "distended just below the pointed apex, the distension being broader on one side of the median rib and having here a deep concavity, the lower edge of which forms what in the light microscope is seen as the lower of the two teeth. The upper tooth is seen to consist of two separate teeth, one formed by the upper edge of the concavity, the other possibly an enlargement of the median rib. The latter may be provided with other few small pointed teeth in the region of the distended portion of the bristle. The apical edge of the lower tooth is thickened by a folding. The shaft of the bristle below the distention may have a few widely spaced teeth." (ASMUND 1959, p. 30). The other bristles are unilaterally serrated (see fig. 4).

d) var. ***inermis*** FOTT var. nova Tab. III

Synonymum:
Mallomonas tonsurata TEILING var. *alpina* (PASCHER et RUTTNER) KRIEGER sensu FOTT, 1955, p. 280—282, tab. 5.
Differt a var. *acaroides* spinis simplicibus, subtiliter serratis, et cystis levibus.

Cells ovoid to ellipsoid, 15—20 μ in length, 7.5—9.5 μ in breadth, bearing patulous bristles only in the anterior part of the body. Scales oval, in the anterior part of the body tripartite (4.3—4.5 μ × 2.4—3.2 μ), the posterior scales smaller (2.4—2.6 μ × 3.2—4 μ), bearing no bristles, dome lacking, showing a rhombic frame of ribs. Bristles slightly bent, gradually attenuated, in the light microscope inconspicuously, in the electron microscope distinctly serrated, without helmet-shape at the tip. Cysts spherical, flattened at the pore, without a surrounding collar, smooth, structure-less, 10—15 μ in diameter.

Occurrence. In a small swamp, Břve, near Prague, Czechoslovakia, 11th November 1950.

Note. By using the key of HUBER-PESTALOZZI 1941 I determined this *Mallomonas* as *M. tonsurata*, considering that the external appearance of the flagellate was the same and the scales were distinctly tripartite, with V-rib. Later, I noticed that the electron micrographs of my species are identical with the micrographs of ASMUND 1949 and BRADLEY et HARRIS 1960, which latter belong to *M. acaroides*. The differences from the other varieties consist largely in the morphology of cysts and in the lack of helmet-shaped bristles, and on these grounds, therefore, I transfer the species to *M. acaroides* as a new variety.

Mallomonas crassisquama (ASMUND) FOTT comb. nova

Tab. IV

Mallomonas acaroides PERTY em. PASCHER, KRIEGER et CONRAD var. *crassisquama* ASMUND 1959, p. 32—35, Fig. 30 a—e (Basonym); TAKAHASHI 1961, p. 406—7, fig. 1—19.

Cellula ovalis vel ovatus, 14—20 μ longa, 9—12 μ lata, intus var. *striatula* similis. Squamae ovales vel ellipticae, 3,5—7 μ longae, 2,5—5,5 μ latae, crassae, a latere visae percurvae, cruribus cristae V-formis saepe valde concavis, inter cristam et marginem posteriorum crasse striatae, medio crasse reticulatae, posticae parvae, obliquae, setis destitutae, spinis saepe armatae, reliquae setas var. striatulae similis, 13—32 μ longas gerentes. Cystae ignotae (ASMUND l. c. p. 32).

Occurrence. Denmark in lakes, Finland, Alaska (ASMUND 1959), Japan in lakes (TAKAHASHI), Czechoslovakia in ponds (tab. IV*b, c* in this paper).

Note. ASMUND described this species as a variety of *M. acaroides*. She is of the opinion "that body shape, size and content and structure of domes and scales and bristles are identical". This is true, but the scale-patterning is quantitatively quite different. In both species the scales are tripartite, but they differ fundamentally in the submicroscopical morphology of the shield. In *Mallomonas acaroides* the shield is quite smooth, bearing no structure, except for the perforations of many pores as in the majority of species. On the other hand, the shield of *M. crassisquama* is covered by a well developed network of meshes which projects considerably above the scale surface. The meshes are very much alike, pentagonal, hexagonal, or irregular, covering the whole area of the shield. The connecting struts are stout and reach the folded rim of the flange only in the proximal part of the scale. In *M. acaroides*, however, these struts are short projections, disappearing on the flat of the flange and only here and there reaching the rim of the flange. The whole submicroscopical structure in *M. acaroides* is much finer than in *M. crassisquama*. Moreover, this species differs further from *M. acaroides* in possessing posterior scales with long spines that are a quite different feature from the bristles, being an outgrowth of the scale. Figures 30 *c d* in ASMUND (1959) give clear evidence of this and such spines have never been recorded in *M. acaroides*.

M. crassisquama seems to be very common in plankton and is widespread in the world. ASMUND (1959) notes many localities in Denmark, a record from Finland and from Alaska (ASMUND 1961). Specimens were found during every month of the year, at temperatures from 1—23 °C, the most common temperature range being 10 °C to 15 °C. The association of the type locality, Bondedam in Denmark, March 29th 1948, was a flagellate-diatom association dominated by several *Synura* species, *Dinobryon divergens* IMHOF and *Synedra acus* KÜTZ.

By chance the locality in Czechoslovakia, where I found this species, is a pond Polnička near Dářsko, the plankton community of which was dominated in August 1955 by *Synura spinosa* KORSH. and *Melosira ambigua* (MÜL.) GRUN. In addition there were other species of Algae which might characterise the community: *Asterionella formosa, Tabellaria flocculosa, Ceratium hirundinella, Anabaena affinis, Dictyosphaerium pulchellum, Gonyostomum latum, Trachelomonas* spec. div., *Cryptomonas curvata* et spec. div., *Centritractus belonophorus* etc.

In Japan the species was found in lakes of the Asahi mountains in Yamagata prefecture. The plankton of the lake Otori-ike is inhabitated by a *Dinobryum cylindricum - Holopedium gibberum* association, with admixed *Synura sphagnicola, Tabellaria fenestrata, Mallomonas tonsurata, M. akrokomos, Staurastrum* sp., *Micrasterias denticulata*, etc. (TAKAHASHI 1961).

Mallomonas zellensis species nova

Tab. V

Cellulae cylindricae, superne angustatae et truncatae, basi late rotundatae. Longitudo 30—45 μ, latitudo 10—14 μ, plerumque 11 μ.

Squamae ellipsoideae, marginibus crassis et V-structuris conspicuis. Imago electrono-microscopica squamae: Squama tota subtiliter porosa. Pars centralis irregulariter areolata. V-structura magna, proxime cum tectulo. Margo squamae transverse costata. Dimensiones squamarum 7,2—7,5 μ × 4,8—5,2 μ.

Spinae rectae, solum paulo curvatae, marginibus subtiliter serratis, 40—50 μ longae.

Protoplastus communis: chromatophor solus, bipartitus, flagellum unum, brevius, aliquot (usque ad 5) vacuolae pulsantes in parte posteriore cellulae, granum ellipsoideum chrysosae plurimis guttis olei circumdatum.

Habitatio: in planctone lacus Zellsee, Austria 3. 9. 1959.

Cells cylindrical, anterior end somewhat attenuated and truncate, posterior end broadly rounded. Length 30—45 μ, breadth 10—14 μ, mostly 11 μ. Chromatophore as usual parietal, composed of two parts. Flagellum short, some contractile vacuoles (about 5) in the posterior end of the protoplast, many oil droplets around the ellipsoidal chrysose body.

Scales elliptical, with a V-structure, lying across the body, in the light microscope the V-figure composed of two stout ribs, forming a distinct hood. Connecting struts numerous (about 10 per side), going from the arms across the flange, to its edge, which is upwardly folded. Shield covered over its entire surface with a network of irregular meshes, projecting above the level of the shield. Central meshes irregularly pentagonal, the meshes adjacent to the ribs, elongated tetragonal. Whole scale perforated by numerous pores. Dimensions of scales: 7,2—7,5 μ × 4,8—5,2 μ.

Bristles numerous, over all the body, narrow, only slightly bent, in the light microscope finely serrated, pointed at the end. Length 40—50 μ.

Occurrence. In plankton of Zeller See, Austria, collected 3rd September 1959.

Note. *M. zellensis* sp. nova belongs to the group of *Mallomonas* species that have numerous bristles over the entire body and the scales of which display a distinct V-structure. Such species occur often in the plankton of lakes and they cannot be determined by light microscopy alone. When using HUBER-PESTALOZZI's key, I found *Mallomonas elongata* REVERDIN as the nearest species, but in the meantime, ASMUND (1959) examined a *Mallomonas* species from Lake Maggiore in Italy and also identified it as *M. elongata*. She took electron micrographs of its scales which are quite different from those of my species from Austria. Disregarding the fact that *M. elongata* is twice as long as *M. zellensis*, the external morphology and appearance of the two species is similiar. The submicroscopical structure of scales, however, exhibits an entirely different pattern. The scales of *M. elongata* have no meshes on the shield, no connecting struts, a different form of V-structure, a small hood, etc.

On the basis of these facts, I think, the establishing of a new species is justified, even when it is defined only by the electron micrographs of its scales. Comparing scale-structure of *M. zellensis* spec. nova with that of *Mallomonas* species known to date, there is only one species near to *M. zellensis*. It is *M. crassisquama* (ASMUND) FOTT comb. nova, the electron micrograph of the scales of which was taken by ASMUND (1959, fig. 30e) and subsequently recognized by me (see plate IV in this paper). *M. crassisquama* also possesses tripartite scales but the network on the shield is made up of more or less regular pentagonal or hexagonal meshes, the connecting struts are less numerous (5—6) and those at the proximal end are short, not reaching the rim of the flange. *M. crassisquama* differs from *M. zellensis* sp. nova in bearing spines on the posterior scales. The spines may be short or quite long, similar to the bristles but differing from them in that they are firmly affixed to the scale. Such spines are lacking in *M. zellensis* sp. nova. In addition, the cells of *M. crassisquama* are smaller (13—32 μ) than those of *M. zellensis* (30—45 μ).

Mallomonas leboimei BOURRELLY

Tab. VI

Mallomonas leboimii BOURRELLY 1947, p. 4—5, tab. 3 : 12—16 (diagnosis, ikonotypus); HARRIS 1953, p. 90, fig. 6—8; HARRIS et BRADLEY 1957, p. 41—42, tab. 1 : 1—3; BOURRELLY 1957, p. 194, fig. F : 3—6, G : 13; ASMUND 1959, p. 25—28, fig. 24—25; HARRIS et BRADLEY 1956, p. 1—3 (sep.), fig. 2.

Synonymum:

Mallomonas sphagnicola NYGAARD 1949, p. 126—128, fig. 68.

Cells elongate ellipsoid or ovoid, 35—40 μ in length, 10—22 μ in breadth. Flagellum as long as the body, two parietal chromatophores, no stigma.

Scales tripartite (10—12 $\mu \times 6$—7 μ), dome prominent, V-rib stout with transverse struts distinctly visible in the light microscope, shield ornamented with a characteristic submicroscopical structure.

Bristles slightly bent, apparently unilaterally serrated, 30—50 μ in length, over the entire body.

Occurrence. France in Fontainebleau (BOURRELLY 1946), England near Reading (HARRIS 1953, HARRIS et BRADLEY 1957), Denmark in lakes (NYGAARD 1949, ASMUND 1959) and Czechoslovakia in South Bohemia (FOTT in this paper).

Note. *Mallomonas leboimei* is the most easily recognized species of this genus owing to the peculiar structure of its scales, as seen either in the light microscope or electron microscopically. The species is striking in its large dimensions and in its occurrence in acid bogs with pH 3,7—5. It seems to be distinctly acidophilic. The pattern on its scales is very characteristic and cannot be mistaken for that of any other species of *Mallomonas*. Consequently the species can be determined on the evidence of a single scale, without seeing the flagellate. In this way, by observing only electron micrographs of the scales, I was able to discover this species in the bogs of Czechoslovakia.

We now possess three micrographs of its scales: the first from England, from a study by HARRIS and BRADLEY by means of the carbon replica technique, the second from Denmark, taken by ASMUND and the third from the peat bogs of South Bohemia in the area of Lipno, taken by myself. The patterns of the scales from these three localities are identical. The scale is tripartite, exhibing a clear V-rib with an elongated hood. A characteristic feature is the structure of the shield, consisting of several interrupted transverse parallel ribs, joined together by irregular connecting outgrowths and lying parallel to the rows of perforations. The dome is striated on one half (the left) by 6 ribs, whereas the other half is smooth. The other details are better seen from the micrographs (pl. VI : ab) of scales from various localities taken by the above mentioned authors. *Sphagnum*-bogs with a very low pH are inhabitated in Czechoslovakia with a similar species, *Mallomonas paludosa* FOTT. It is a pronounced sphagnophilic species also, growing only in bogs containing living *Sphagnum*. The species can be differentiated from *M. leboimei* by its smaller dimensions and by the quite different submicroscopical structure of the shield.

The electron micrographs of *Mallomonas* scales were made by Dr. J. LUDVÍK, C. Sc. in the Laboratory for Electron Microscopy of the Czechoslovak Academy of Sciences. My thanks are due to him and to Professor J. WOLF, member of Academy, for permission to the use the electron microscope. I am very grateful to K. HARRIS and A. BERIT for some electron micrographs of *Mallomonas* scales, already published in their papers, which I needed for comparison with my observations. I am indepted to J. FIALA for the light microscope photographs and to P. JAVORNICKÝ for the Latin diagnoses. I also wish to thank to Dr. LEEDALE (Leeds) for reading the manuscript and correcting my English.

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Explanations of plates

Tab. I. — *Mallomonas acaroides* PERTY emend. IWANOFF var. *acaroides*. — This is a typical variety, as has been defined by IWANOFF 1899. (Compare his figure in this paper fig. 3*a*—*c*.) — *a* surface view of the armour of scales, bearing bristles. Evidently all scales bear bristles, but in the drawing not all are figured. *b* bristle and *c* scale as seen in the light microscope. *d* a scale in the electron microscope. *e* scale and bristles taken by the phase contrast. By this technique the transverse struts are discernible and look like elongated dots. It is presumed that CONRAD, when drawing dotted ribs, has in fact seen the struts, lying across them. For this reason I think the V-structure in *M. acaroides* is composed of ribs and not of dots, as is asserted in CONRAD and in determining keys e.g. in HUBER-PESTALOZZI, MATVIENKO etc. — *a*—*c* orig., *d* orig. micrograph of J. LUDVÍK, *e* orig. photo J. FIALA.

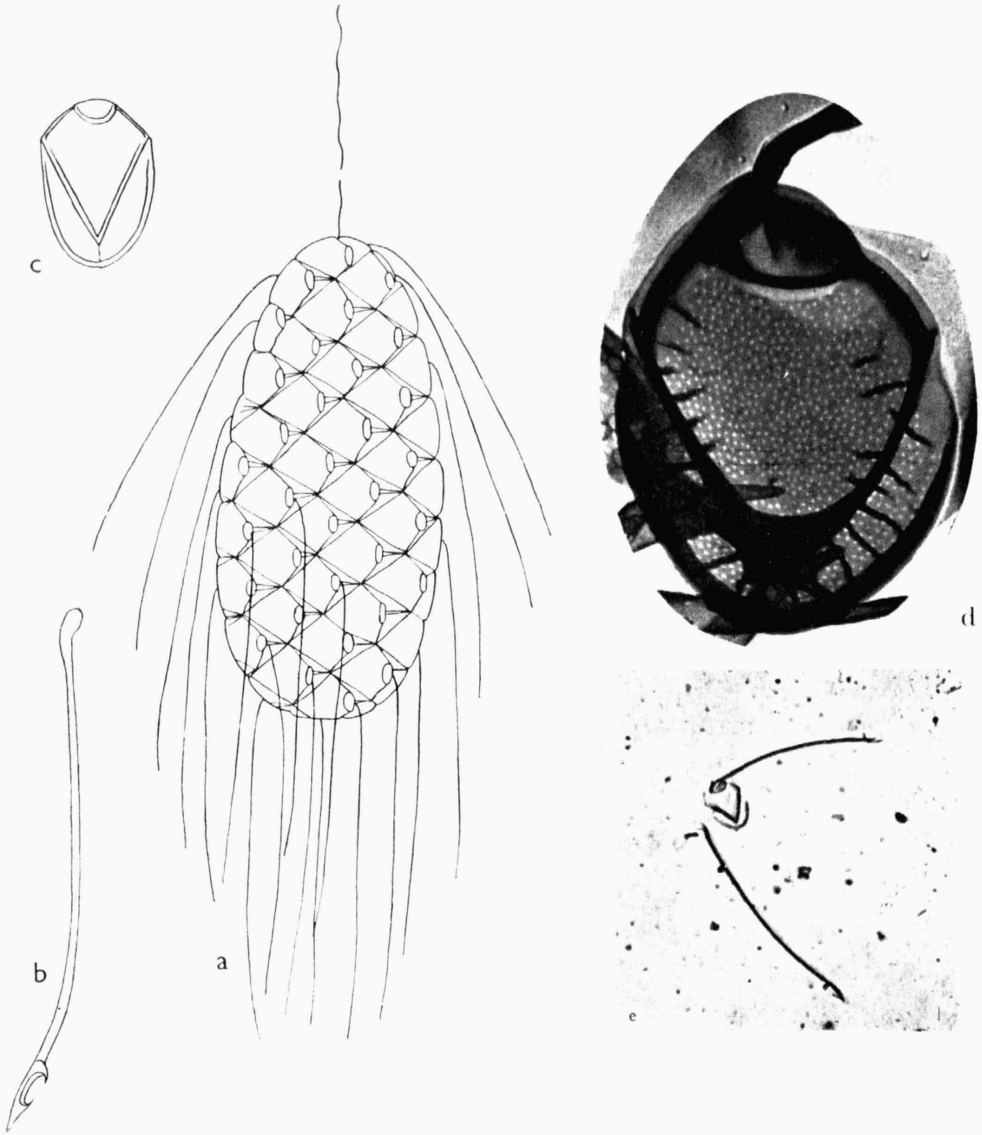
Tab. II. — *Mallomonas acaroides* PERTY emend. IWANOFF. Electron micrographs of scales of various varieties from distant localities showing the identical pattern of their structure. *a* var. *acaroides* (syn. var. *galeata* HARRIS et BRADLEY) from England, Berkshire (after HARRIS et BRADLEY 1960). *b* var. *echinospora* (NYGAARD) FOTT from Denmark (after ASMUND 1959). *c* var. *striatula* ASMUND from Denmark (after ASMUND 1959). *d* var. *inermis* FOTT from Czechoslovakia, Bohemia (orig. micrograph of FOTT et ROZSÍVAL).

Tab. III. — *Mallomonas acaroides* PERTY emend. IWANOFF var. *inermis* FOTT. — *a* surface view of the silica armour of scales. Only scales from the anterior part of the body bear bristles. *b* anterior scale with a spine. In the light microscope the spine is smooth. A posterior scale is without bristle, showing only rhombic frame of ribs. *c* cyst with an envelope of scales surrounding it. The wall of the cyst is smooth, the plug is not discernible. In the middle of the protoplast is an elliptical grain of chrysose. *d* micrograph of the scale from the same material. — *a*—*c* orig. drawings, *d* after FOTT 1955.

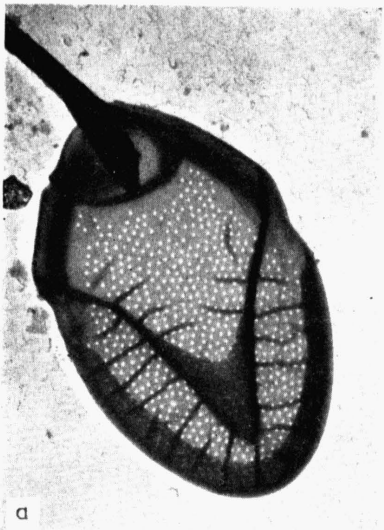
Tab. IV. — *Mallomonas crassisquama* (ASMUND) FOTT. The scales from Denmark (*a*) and Czechoslovakia (*b*, *c*) display the same marking on their surface. *b* rear scale without the dome. — *a* orig. micrograph of B. ASMUND, *b*, *c* micrographs of J. LUDVÍK.

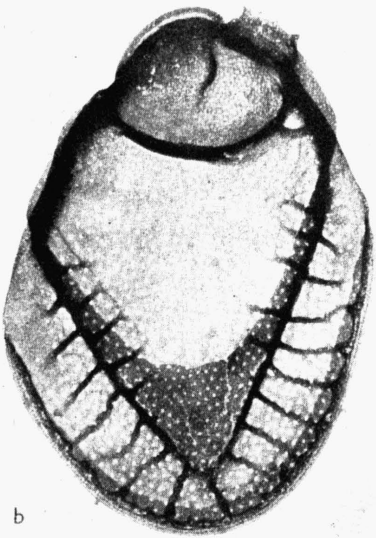
Tab. V. — *Mallomonas zellensis* FOTT spec. nova. — *a* view of the living cell, displaying one bipartite chromatophore, a chrysose grain and many contractile vacuoles in the posterior part of the cell. Scales as seen with a dry system (*b*) and with immersion (*c*). *d* micrograph of a scale. *e* scales and bristles taken with a phase contrast. The negative shows the structure of the shield and the connecting struts, but these details became indiscernible in print. — *a*—*c* orig., *d* orig. micrograph of J. LUDVÍK, *e* orig. photo of J. FIALA.

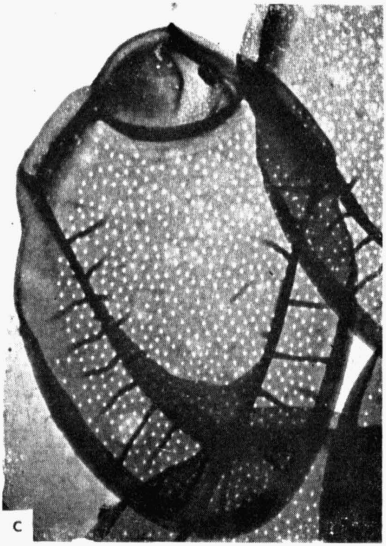
Tab. VI. — *Mallomonas leboimei* BOURRELLY. — *a* scale showing the details of the submicroscopical structure. This micrograph reproduced as negative is one of the best ever made, displaying a great amount of detail of the structure on the scale. Material from Denmark. *b* micrograph reproduced as positive from the material of Bohemia, Czechoslovakia. The white shadow on the scales show clearly how much the dome and the frame-work project above the scale level. — *a* after ASMUND 1959, *b* orig. J. LUDVÍK.

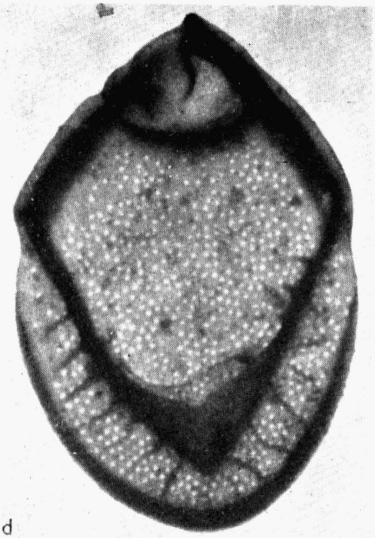


B. Fott: Taxonomy of *Mallomonas* based on electron micrographs of scales

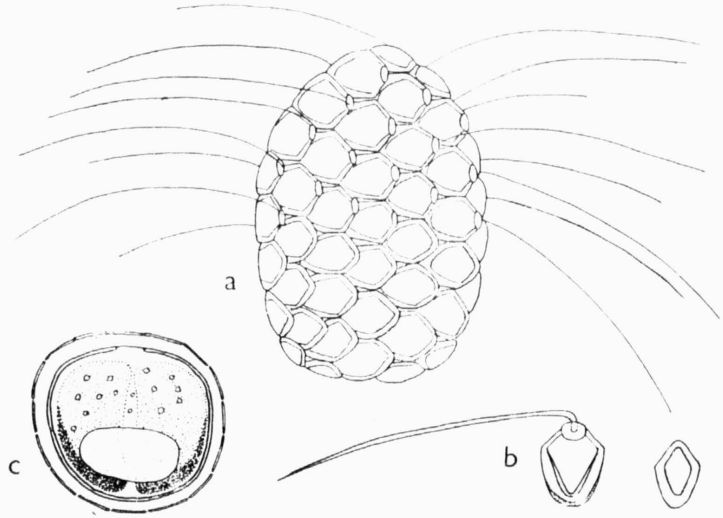


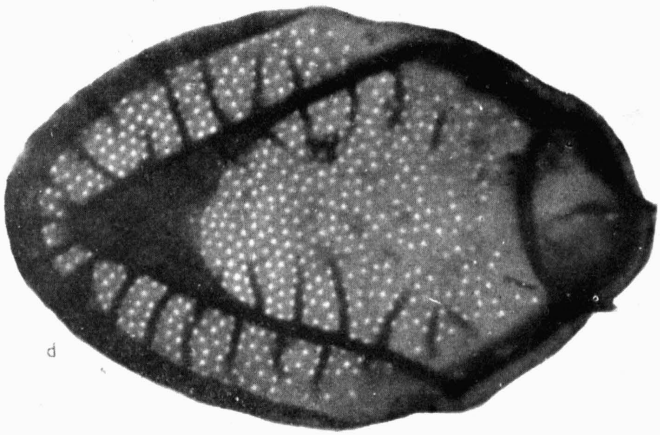




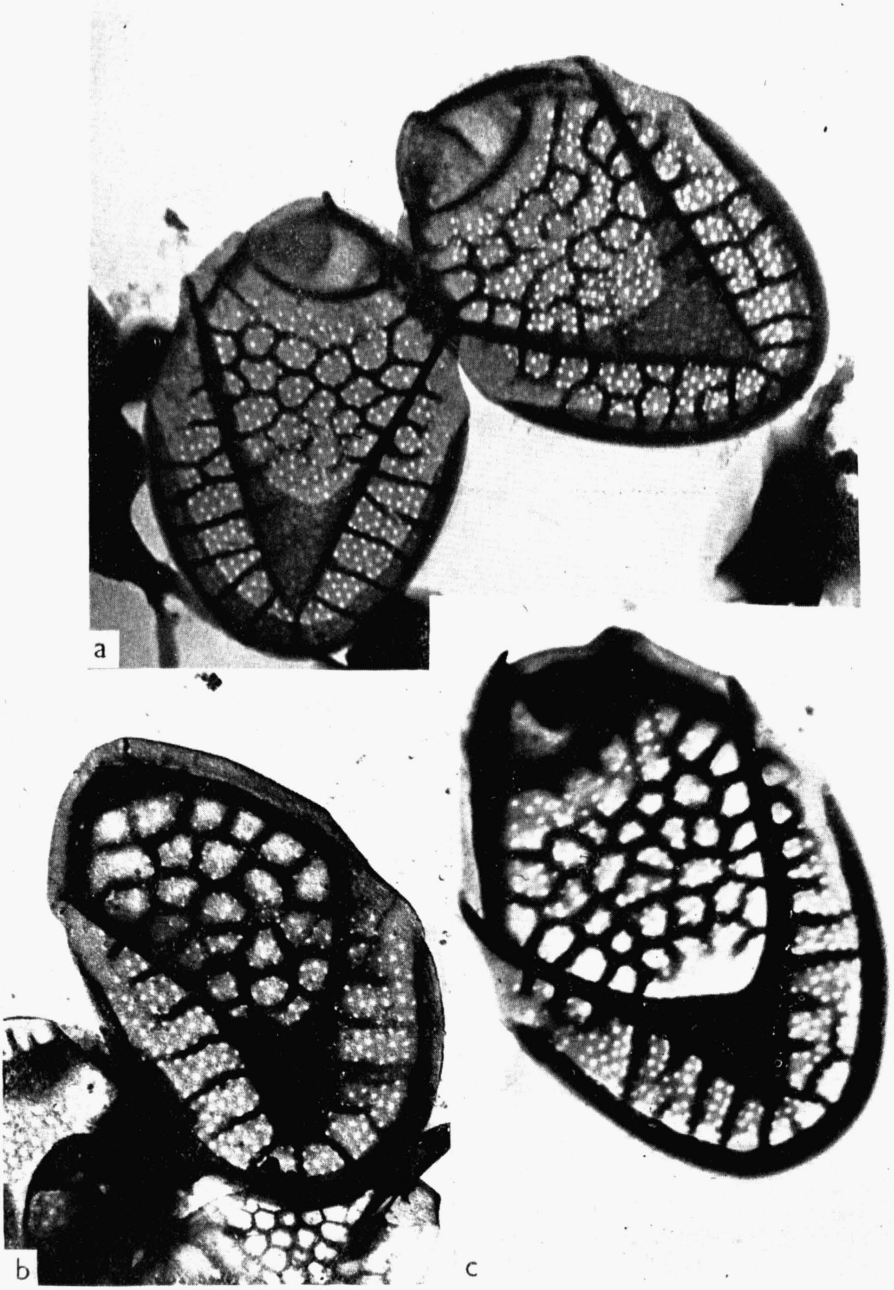


B. Fott: Taxonomy of *Mallomonas* based on electron micrographs of scales

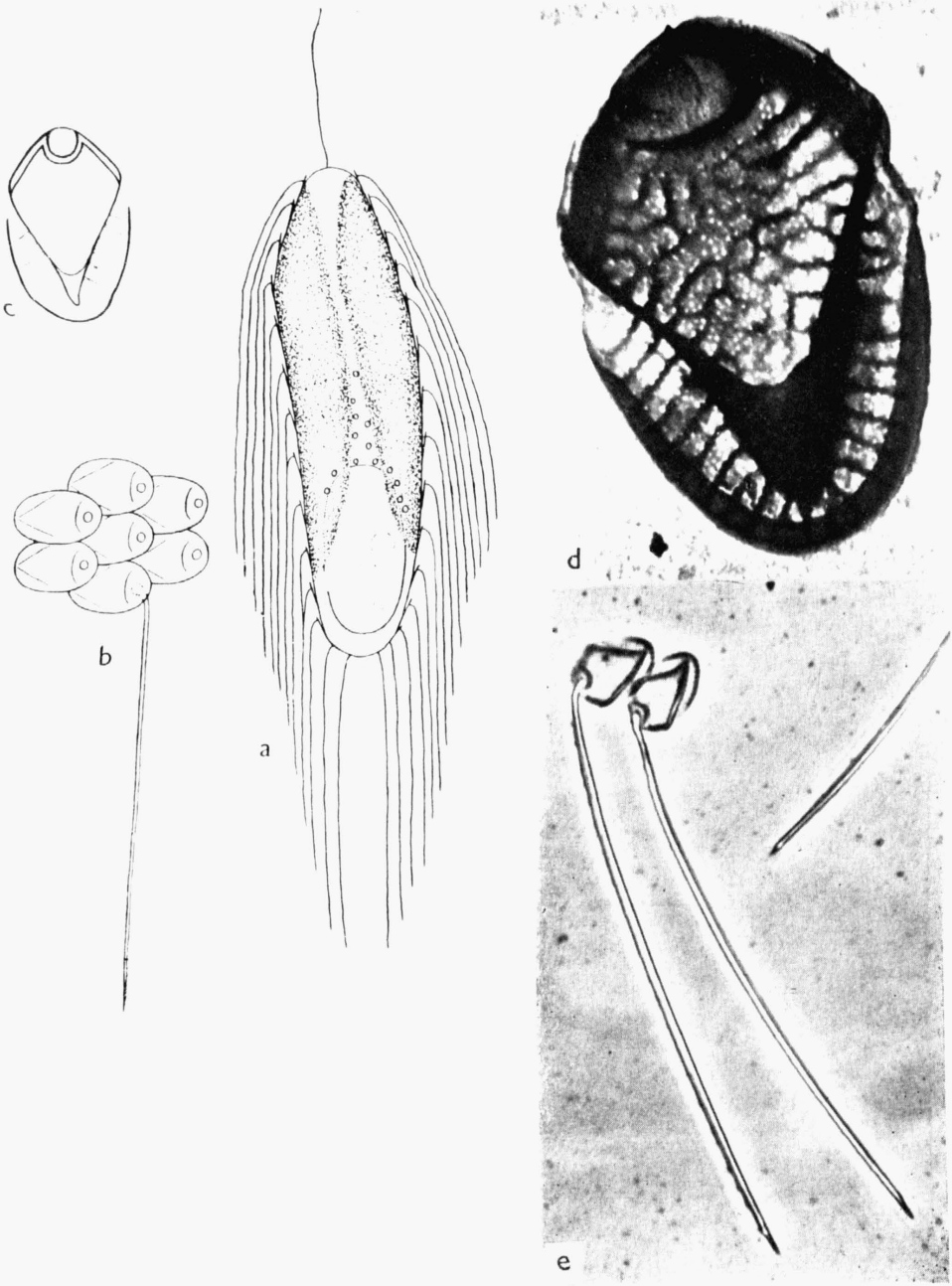




B. Fott: Taxonomy of *Mallomonas* based on electron micrographs of scales



B. Fott: Taxonomy of *Mallomonas* based on electron micrographs of scales



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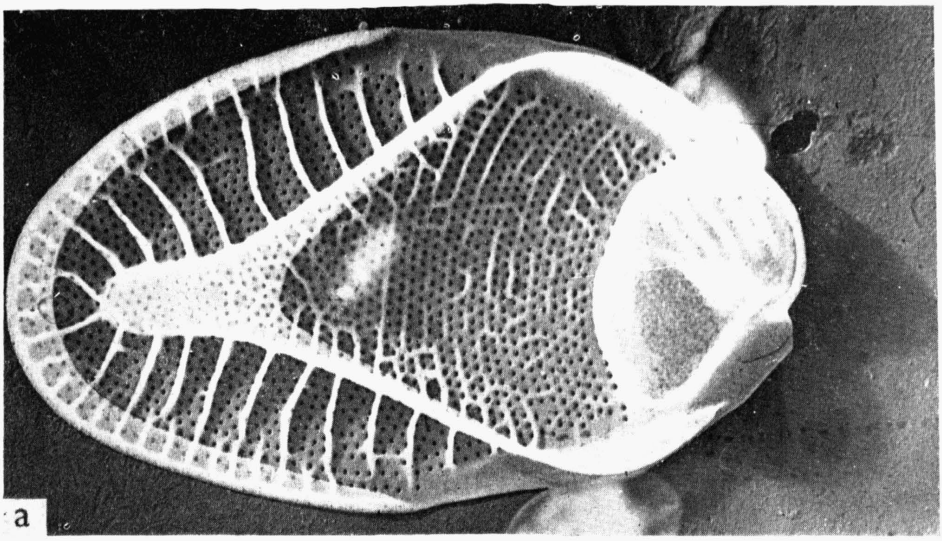

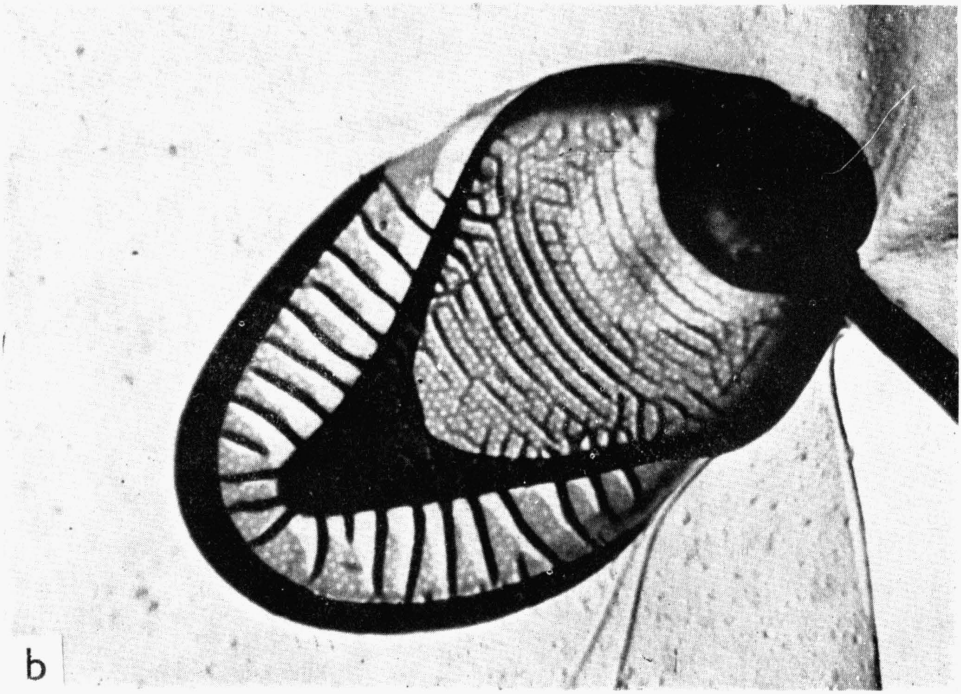

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