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Observations and taxonomy of *Pyramimonas longicauda* (Class Prasinophyceae)*

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A species of *Pyramimonas* collected in the Bay of Dokai, Fukuoka Prefecture, Japan has been examined with both the light and electron microscope. The cells characteristically have an arrow-head or funnel-like shape with well developed anterior lobes and a caudate appendage extending posteriorly. However, there is a wide range of cell shape and the organism can be assigned to either one of the previously described two species, namely, *P. ostendensis* and *P. longicauda* (VAN MEEL 1969). Based on observations with the light microscope of the cultured material, it was concluded that VAN MEEL's two species are conspecific, and *P. longicauda* VAN MEEL was chosen as the correct name for the species. Ultrastructurally, *P. longicauda* is characterized by the shape and the size of scales which coat the entire cell-surface including the flagella. Both the intermediate and the outermost layer body-scales are much larger than those described for any other species and have a characteristic architecture. Four basal bodies are arranged in a rhombic (diamond-shaped) pattern. The pyrenoid matrix is invaded by thylakoids from the anterior side only and it is surrounded by two well developed starch sheaths. On the basis of our observations, an emended diagnosis of *Pyramimonas longicauda* is given.

Key Index Words: *Electron microscopy*; *Prasinophyceae*; Pyramimonas longicauda; Pyramimonas ostendensis; *Taxonomy*

Species of the genus *Pyramimonas* are a common component of the microalgal flora in coastal and estuarine waters and play a significant ecological role in such areas. "Blooms" of *Pyramimonas* species have also been observed many times in various bays in Japan. The taxonomy of this genus at species rank is, however, still confused. Although taxonomic studies have been carried out on several species and considerable amount of knowledge concerning cellular and scale morphology has been acumulated (e. g. NORRIS 1980 for review), there are still many difficulties in delimiting species. Our recent research has been directed towards resolving some of the problems in the genus. The present paper is the second of a series of studies and deals with an unusual species which can be assigned to *Pyramimonas longicauda* VAN MEEL. Observations were made using both light and electron microscopy and, from these an emended diagnosis for the species is given.

Materials and Methods

Seawater samples were kindly collected from the Bay of Dokai, Fukuoka Prefecture, on monthly basis by Mrs Machiko YAMADA of the Kitakyushu Municipal Institute of Environmental Health Sciences, Kitakyushu-shi, and sent to us by express mail. The living specimens grew in enrichment culture

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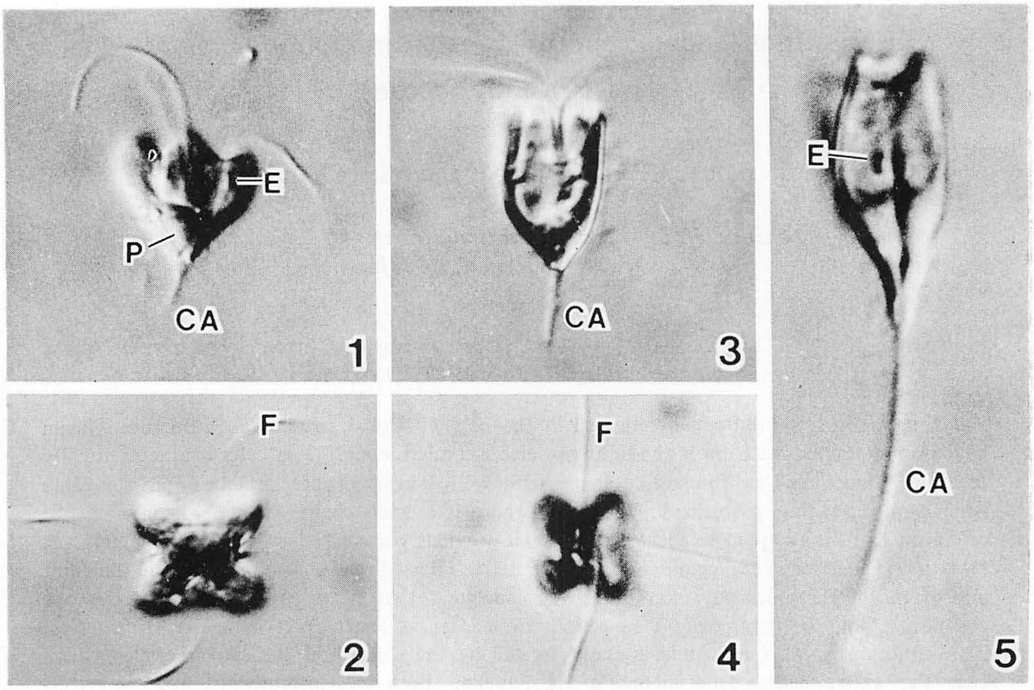


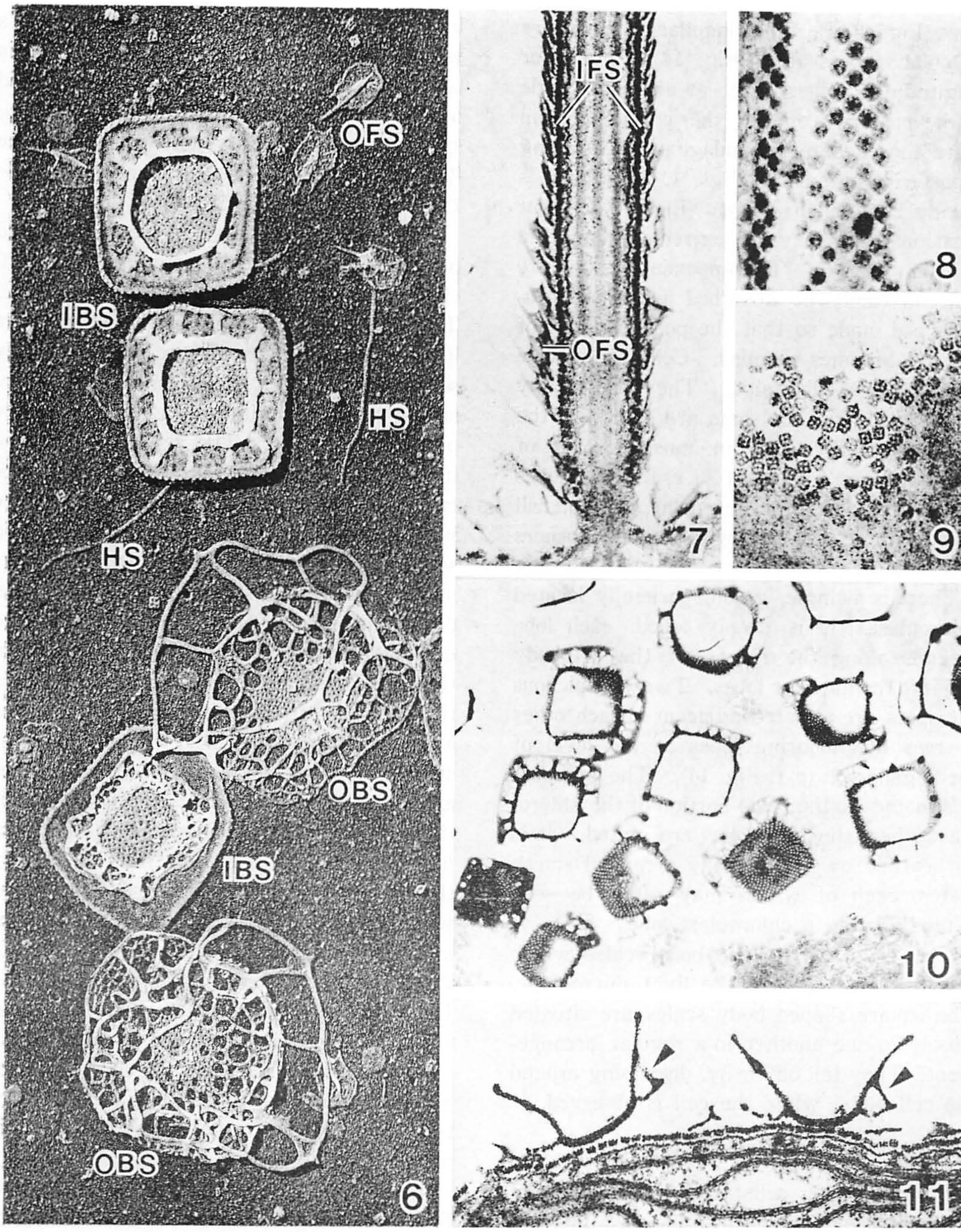
Fig. 1–5. *Pyramimonas longicauda* Light microscopy 1. Lateral view of arrow-head or funnel-like cell; anterior lobes, pyrenoid (P), eye-spot (E) and caudate appendage (CA) are seen. ×1,100; 2. Polar view of arrow-head or funnel-like cell showing flagella (F) radiating out. ×1,100; 3. Lateral view of typical *Pyramimonas*-like cell with caudate appendage (CA). ×1,100; 4. Polar view of typical *Pyramimonas*-like cell. The cell is more or less square in profile with rounded corners. Note the four flagella (F) radiating out in four directions. ×1,100; 5. Cell with extraordinaly long caudate appendage (CA). Two eye-spots (E) situated close to each other are also seen. ×1,600.

of a sample collected on 10 November 1980. Single cells were isolated and inoculated into Erd-Schreiber medium (FØYN 1934). Although not growing rapidly, the culture produced sufficient material to allow light and electron microscopical observations. Preparations for the electron microscopy were same as those described in the previous report (INOUYE *et al.* 1983). For careful observation of the living cells, a drop of 10 mM $NiCl_2$ was added to the medium containing actively swimming cells just before observations were made. This inhibited the flagellar movements without causing damage to the cell structure. Electron microscopy was made with JEOL 1000C and HITACHI H-12.

Observations

Light microscopy

The cell is usually arrow-head or funnel-like in shape. It has four well developed lobes projecting anteriorly and a slender caudate appendage extending posteriorly (Fig. 1). Cells are 16–48 μm long (12.5–20.5 μm excluding the caudate appendage) and 10.0–22.5 μm wide anteriorly. Four lobes extend longitudinally as ridges from the anterior towards the posterior of the cell (Fig. 1). These are well developed so that the cell is cruciform in polar view (Fig. 2). The lobes project anteriorly and give a characteristically concave or invaginated contour at the anterior region. At the bottom of this concave region there is a pit from which four flagella arise and extend in four directions, each passing along the furrow between two



Figs. 6-11. *Pyramimonas longicauda* Electron microscopy 6. Shadowcast preparation of flagellar and body scales (reversed print); *Limulus*-like outer flagellar scales (OFS), hair scales (HS), intermediate (IBS) and outermost (OBS) body scales are seen. Top two IBS are viewed from its distal side and bottom one is viewed from its proximal side. ×26,000; 7. Longitudinal section of a flagellum; inner (IFS) and outer (OFS) flagellar scales are shown arranged in two layers. ×3,000; 8. Tangential section of flagellum showing regularly arranged square to pentagonal inner flagellar scales. ×50,000; 9. Tangential section of body surface showing square-shaped innermost body scales. ×40,000; 10. Glancing section of body scale layers. The intermediate scales are shown cut in various planes. ×18,000; 11. Innermost and intermediate body scales arranged in layers on body surface. Rods interconnecting base-plate and wall of superstructure in intermediate scales are seen (arrow heads). ×27,000

lobes (Figs. 2, 4). The flagellar pit is square in polar aspect (c.f. Fig. 14). The four longitudinal ridges meet at an acute angle at the posterior end of the cell and from there the caudate appendage arises forming a posterior extension (Figs. 1, 3). This is usually 2-4 μm in length (Figs. 1, 2), but occasionally it may be extremely long, up to 25 μm (Fig. 5). The appendage is delicate and can easily be absorbed while observations are made so that the posterior part of the cell becomes rounded. Cells show wide morphological diversity. They are mostly arrow-head-like, but some are similar to the cells commonly seen in most species of *Pyramimonas* (Figs. 3, 4), i.e. the four lobes are less developed and the polar view of cell is more or less square with rounded corners (Fig. 4).

There is a single, green, parietally located chloroplast. It is deeply lobed, each lobe extends along the ridges of the cell-body and into the anterior lobes. Two conspicuous eye-spots are situated adjacent to each other in two neighbouring lobes at the level of the flagellar pit (c.f. Fig. 14). The pyrenoid is situated in the basal portion of the chloroplast where the four lobes are united. It is ensheathed by two laterally arranged starch plates, each of which may often be seen extending into a chloroplast lobe.

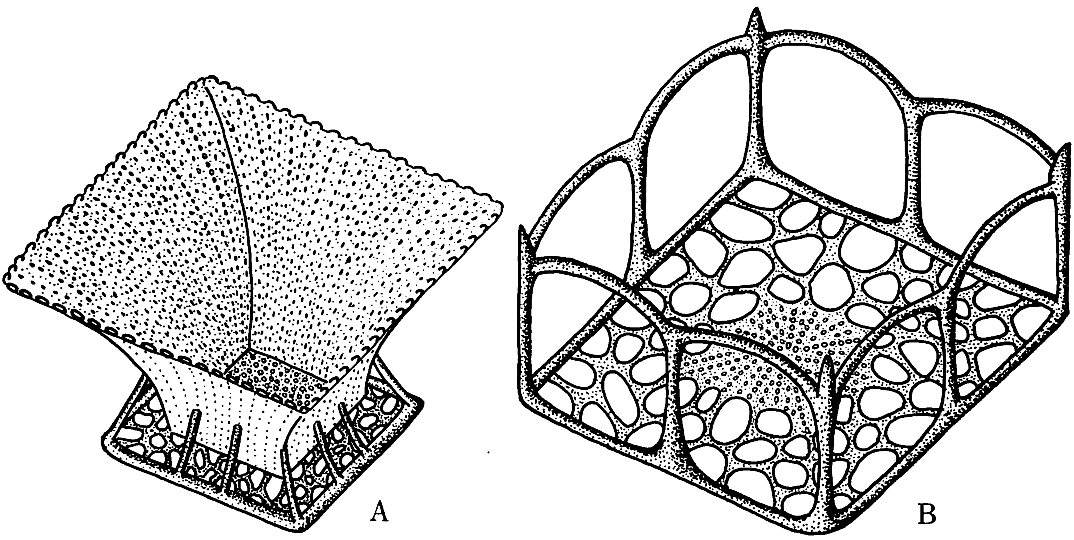
The cells have large body scales which can be seen even with the light microscope. The square shaped body scales are situated closely to one another in a regular arrangement. They fall off easily, dispersing around the cell body, while the cell is observed.

Electron microscopy

P. longicauda cells carry six kinds of scales, three of which are disposed in three layers on the flagella, the other three types in three layers on the cell-body surface. The inner (proximal) flagellar scales against the flagellar surface are square to pentagonal, ca. 40 nm on each side, with a raised rim and small central boss (Figs. 7, 8). The outer layer flagellar scales resemble a horse-shoe crab (*Limulus*) and are 400-500 nm long including spines. They have a spider's web pattern on the surface although this is often obscure. These scales are arranged on top of the inner layer, their projecting spines pointing distally with respect to the flagella (Fig. 7). The hair scales are 0.8-1.2 μm in length (Fig. 6).

The innermost body scales are deposited on the outer surface of entire cell body, including the caudate appendage (Fig. 11). They are similar to the inner flagellar scales in both shape and size but are more obviously square in shape, ca. 45 nm on each side, consisting of a raised rim and a central boss or projection (Fig. 9). The scales of both the intermediate and the outermost layers are large and have characteristic structure. The intermediate body scales are composed of a square shaped baseplate and a basket-like superstructure (Figs. 6, 11). The baseplate, 0.6-1.0 μm long on each side, consists of two distinct portions, each of which has perforations arranged in a characteristic pattern. In the central portion, which is square-shaped and corresponds to the bottom of the superstructure, there are a number of fine holes arranged regularly, while in the outer portion there are larger holes arranged irregularly (Figs. 6, 10). Twelve rods arise from the margin of the base-plate reaching to the wall of the superstructure though in whole-mounted scales these can only be seen in those displaying their distal face (Figs. 6, 11). The perforation pattern in the superstructure is similar to that in the central portion of the base-plate. There are also numerous fine holes on the surface, although they are much finer than those of the base-plate.

The scales of the outermost layer are box-like, consisting of a square base-plate and four sides made up of a framework of rod-like elements (Fig. 6). The base-plate, 1.0-1.2 μm on each side and similar to that of the intermediate body scale, consists of two portions, a central square-shaped portion with numerous fine holes and an outer irregularly reticulated portion (Fig. 6), which are less distinctly delimited than those of



A B

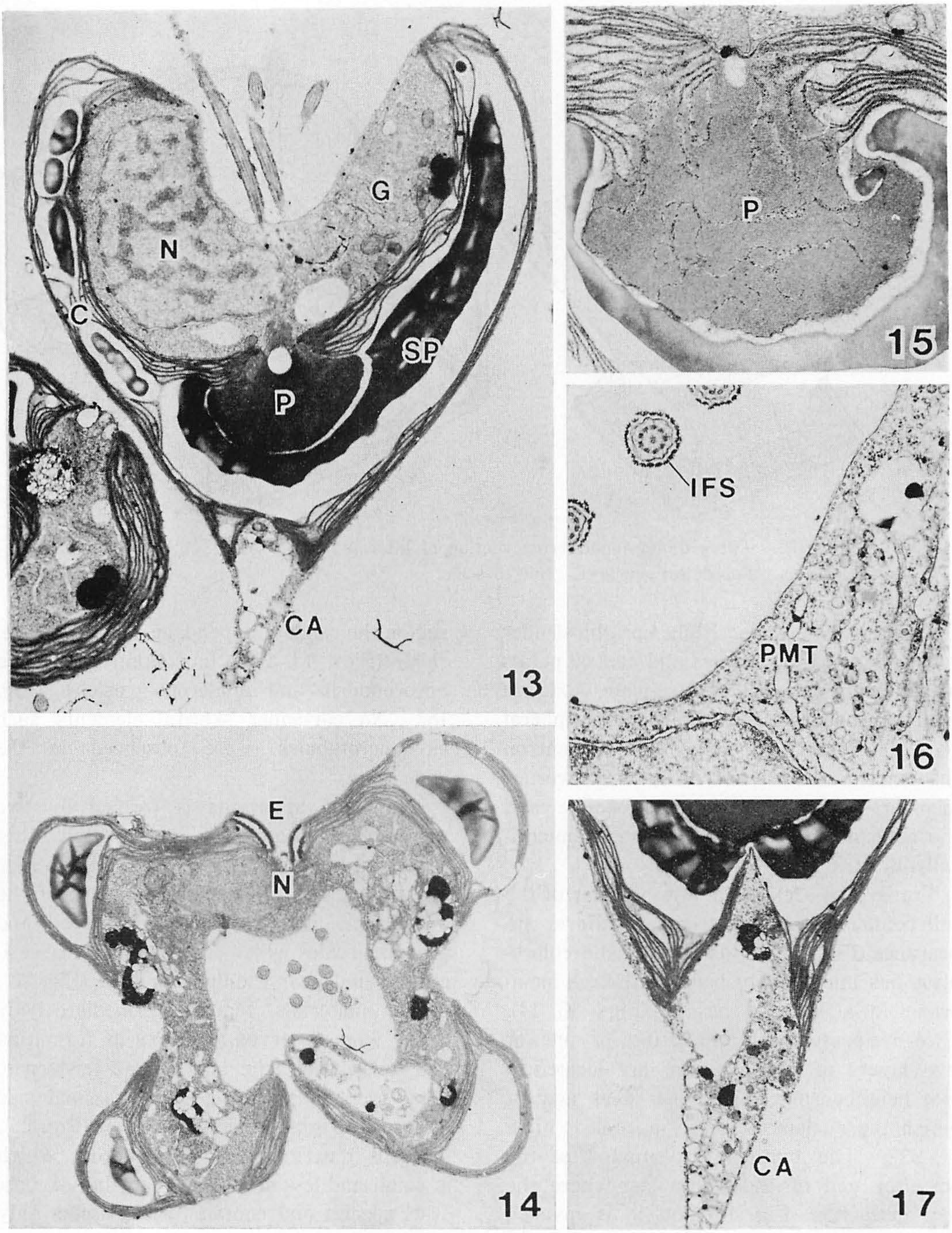
Fig. 12. Three dimensional reconstruction of intermediate (A) and outermost (O) body scales. For detail see text. Not to scale.

the intermediate scale. Eight upright slender rods arise from the corners and central points of the margins of the base-plate and are linked to one another distally by peripheral rods (Fig. 6). Small spines are present on the extreme distal ends of the four corner members (Fig. 6). The intermediate and the outermost body scales are diagrammatically illustrated in Fig. 12.

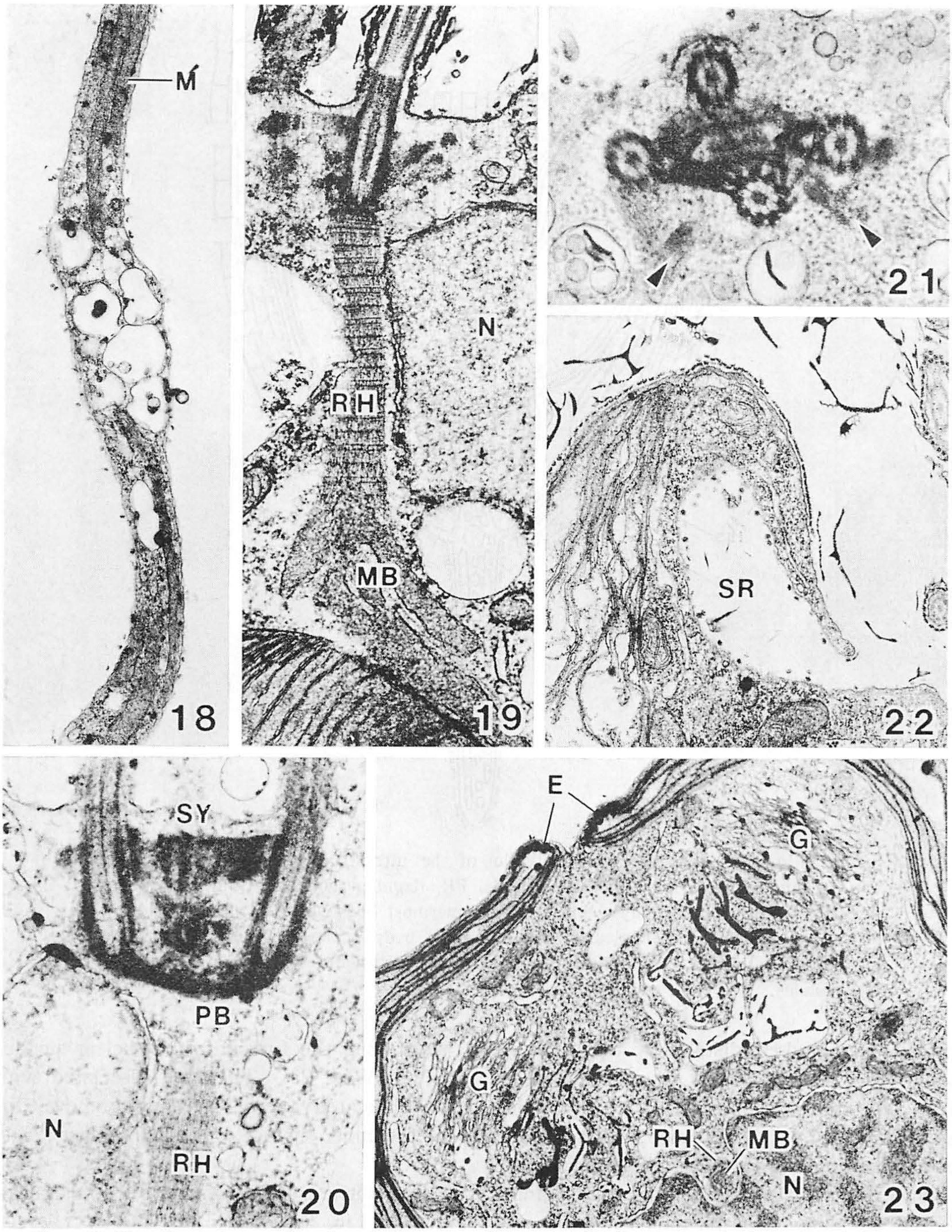
Transverse sections at the anterior of the cell confirm its characteristic cruciform appearance (Fig. 14). Each lobe of the chloroplast lies immediately beneath the cell membrane in a lobe of the cell (Figs. 13, 14). Two eye-spots, each consisting of one or two layers of plastglobules, are located in two neighbouring chloroplast lobes against which the nucleus is closely apressed (Figs. 14, 23). The pyrenoid is situated at the posterior end of the chloroplast where the four lobes fuse (Fig. 13) and it is invaded by thylakoids from the anterior side (Fig. 15). It is surrounded by two well developed starch plates (Figs. 13, 15) each of which has two plate-like projections extending into anterior lobes of the chloroplast (Fig. 13). The chloroplast has a conical invagination at the extreme posterior end which is occupied by vesicles (Figs. 13, 17). From this region the caudate appendage extends posteriorly (Figs. 13, 17). It contains elongated mitochondria and numerous vesicles (Fig. 18). No particular skeletal elements such as microtubules were observed in the appendage.

The Golgi apparatus is formed by two dictyosomes located opposite to each other separated by the flagellar pit and flagellar bases (Fig. 23). The maturing face of the dictyosome always faces the inward and produces scales which are released into vesicles located near the flagellar base (Fig. 23). In our materials, many intermediate body scales were observed at stages of formation and release by the dictyosome cisternae. They are released with their proximal side directed towards the flagellar bases (Fig. 23). There is in each cell a scale reservoir, which is small and less developed than that of most other species and contains small scales only (Fig. 22).

Numerous evenly distributed microtubules (more than 200) are arranged longitudinally along the flagellar pit beneath the plasmalemma (Fig. 16). Four basal bodies are arranged at the base of the flagellar pit in a rhombic (diamond-shaped) pattern (Fig. 21). Those situated on the short axis of the



Figs. 13-17. *Pyramimonas longicauda* Electron microscopy 13. Median longitudinal section of a cell showing major cell components: chloroplast (C), caudate appendage (CA), Golgi apparatus (G), nucleus (N), pyrenoid (P) and associated starch plate (SP). ×5,200; 14. Transverse section of a cell showing clearly four cell and chloroplast lobes, two eye-spots (E) situating in two neighbouring lobes against which nucleus (N) is apressed. Note that the flagellar pit is angular, more or less square in transverse section. ×5,000; 15. Pyrenoid matrix invaded by thylakoids from anterior side only. ×10,000; 16. Transverse section cut through flagellar pit. Pit microtubules (PMT) are seen arranged around the plasmalemma of the pit. Inner flagellar scales are also seen situated on the flagellar surface. ×18,000; 17. Longitudinal section of posterior portion of a cell showing posterior groove of chloroplast and the caudate appendage containing numerous vesicles. ×5,300



Figs. 18-23. *Pyramimonas longicauda* Electron microscopy 18. Caudate appendage containing vesicles and elongated mitochondria (M). ×13,000; 19. Longitudinal section of a cell showing association between basal bodies (B), rhizoplast (RH), nucleus (N), microbody (MB) and pyrenoid (P). ×27,000; 20. Longitudinal section of flagellar apparatus. Two basal bodies are interconnected with synistosome (SY) and proximal band (PB). The nucleus (N) and rhizoplast (RH) are located below the basal bodies. ×33,000; 21. Transverse section of flagellar apparatus. Four basal bodies are arranged in diamond-shaped pattern and interconnected by the synistosome and numerous other bands. Two microtubular roots are also seen (arrow heads). ×31,000; 22. Poorly developed scale reservoir (SR) containing a few scales. ×16,000; 23. Transverse section of cell through eye-spots (E) showing Golgi apparatus (G) producing scales. The rhizoplast (RH) and associated microbody (MB) situated in a furrow on the nucleus (N) are also shown. ×9,500

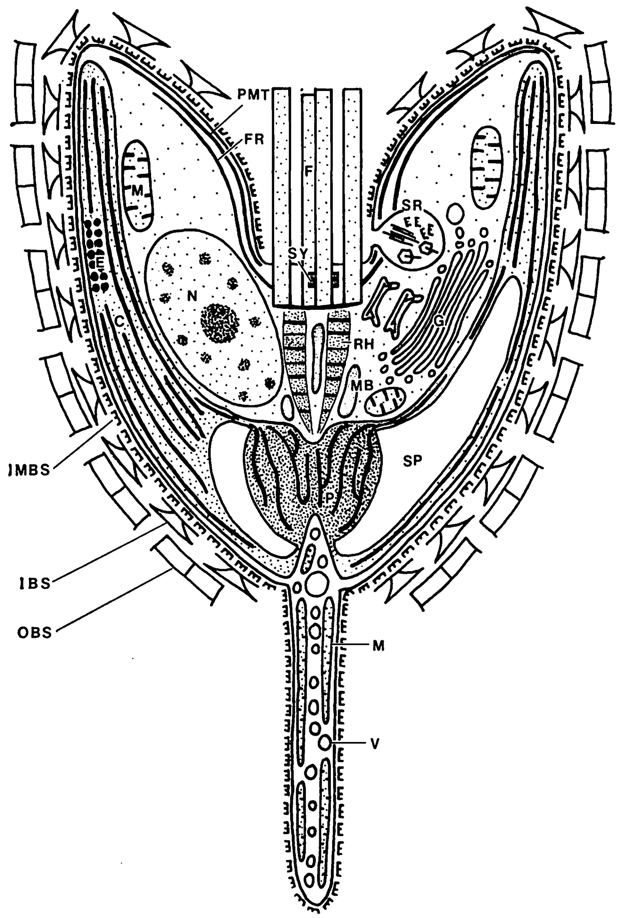


Fig. 24. Diagrammatic illustration of the ultrastructure of *P. longicauda*. C: chloroplast, E: eye-spot, F: flagella, FR: flagellar roots, G: Golgi apparatus, IBS: intermediate body scale, IMBS: innermost body scale, M: mitochondria, MB: microbody, N: nucleus, OBS: outermost body scale, P: pyrenoid, PMT: pit microtubules, RH: rhizoplast, SR: scale reservoir, SY: synistosome, V: vesicles.

rhombus are linked distally by the synistosome (Figs. 20, 21). All four basal bodies are connected by numerous bands to one another (Fig. 21). Four groups of microtubules, flagellar rootlet microtubules, originate below the synistosome and extend in four directions along the proximal side of the pit microtubules. Two such roots can be seen in Fig. 21 but the number of microtubules composing each root is still not clear. The basal bodies are connected by dense bands at their extreme proximal ends (Fig. 20) and, from these, striated bands (rhizoplasts) originate and extend posteriorly passing along the furrow in the nuclear surface (Figs. 19, 20, 23). They are associated with an elongated microbody and extend as far as the inner surface of the chloroplast (Figs. 19, 23).

The ultrastructure of the cell is diagrammed in Fig. 24.

Discussion

The alga described in this paper is very similar to *Pyramimonas ostendensis* and *P. longicauda*, simultaneously described from Belgium by VAN MEEL (1969). According to the author, these two species differ from each other in the shape and size of the cell: *P. ostendensis* is 32×24 μm, funnel-like, with caudate appendage, whereas *P. longicauda* is typical *Pyramimonas*-shape, with distinct caudate appendage and measures 28×12.5 μm. In the course of the study, we have found that the cell shape was very changeable and, at least, two forms which corresponded with the two taxa of VAN MEEL, occurred in the cultures started from single cells. Usually the cells were arrow-head or funnel-like in shape when the cell lobes were well developed, whereas the so-called "typical *Pyramimonas*-shape" was exhibited when the lobes were less developed. It was also noticed that the cells showed the wide size range (from 16 to 48 μm in length and 10 to 23 μm in width) which spanned the cell sizes given by VAN MEEL for both *P. ostendensis* and *P. longicauda*. From this evidence, we are of the opinion that the two taxa of VAN MEEL are conspecific and, in turn, our alga is the same as that of VAN MEEL. However, one important difference exists between our specimen and those described by VAN MEEL, i.e., the number of eye-spots. Both *P. ostendensis* and *P. longicauda* have a single eye-spot whereas our alga has two, although they are situated close to each other. In general, the number of eye-spots within a species of *Pyramimonas* is constant so that this difference might be sufficient to separate these algae at specific or infraspecific rank. However, since the alga described here is so similar to those of VAN MEEL, and since there are no features to separate them other than the number of eye-spots, we consider our form to be conspecific with the earlier taxa, the differences between them probably being due to morphological plasticity. As to the species name for this alga, we would like to choose *P. longicauda* as the correct name since the epithet "*longicauda*" indicates more properly its peculiar characteristics. An emended description of the species is given at the end of the paper.

With regard to ultrastructural features, scale morphology has been well studied in the genus. In their investigations of *Pyramimonas* species, NORRIS and PIENAAR (1978) concluded that the flagellar and body scales characters are reliable enough to be used as diagnostic criteria for identification of species. In addition to these, the following features probably have taxonomic significance and will be used for delimiting species: 1) Flagellar apparatus including arrangement pattern of basal bodies, 2) presence or absence of trichocysts, 3) degree of development of scale reservoir, 4) the presence or absence of the caudate appendage and 5) the pattern of thylakoids into the pyrenoid matrix.

We may comment briefly on each of these features. (1) Flagellar apparatus: As has been emphasized in the previous report, the four-flagellated *Pyramimonas* species can be classified into two groups based on the ultrastructure of flagellar apparatus. The first group is characterized by basal bodies arranged in rhombic (diamond-shaped) pattern and the absence of a fibrous band and include *P. obovata* N. CARTER (MELKONIAN 1981), probably *P. orientalis* BUTCH. (MOESTRUP and THOMSEN 1974), *P. disomata sensu* NORRIS and PIENAAR (1978) (unpublished observation) and *P. longicauda* (present paper). The second group is characterized by basal bodies arranged in 3-1 patten and the presence of a fibrous band connecting three of four basal bodies. *P. parkeae* NORRIS et PEARSON (NORRIS and PEARSON 1975), *P. lunata* INOUYE *et al.*, (INOUYE *et al.* 1983), *P. grossii* PARKE and some other unidentified species (unpublished observations) belong to this group. (2) Trichocysts: To date this organelle has been found only in five species, namely *P. grossii* (MANTON 1969), *P. parkeae* (NORRIS and PEARSON 1975), *P. virginica* PENNICK (PENNICK 1977), *P. cirolanae* PENNICK (PENNICK 1982) and *P. lunata* (INOUYE *et al.* 1983). We think that trichocysts probably occur only in species which belong to the second groups as classified on flagellar apparatus (see above), although *P. virginica* and *P. cirolanae* need further study before this opinion can be substantiated. (3) Scale reservoir: A well developed scale reservoir has been found in several species including *P. amylifera* CONRAD (MANTON 1966), *P. tetrarhynchus* SCHMARDA (MANTON 1968), *P. parkeae* (NORRIS and PEARSON 1975) and *P. lunata* (INOUYE *et al.* 1983). There is no correlation between cell-size and degree of development of the scale reservoir. Thus it is poorly developed in *P. longicauda* in spite of its large cell size and rather well developed in smaller species such as *P. grossii* and *P. obovata* (MELKONIAN 1981). In order to evaluate the taxonomic significance of this organelle, further investigations are required. (4) Caudate appendage: This structure appears to be restricted in its distribution. To date, *P. torta* CONR. et KUFF. (CONRAD and KUFFERATH 1954), which differ from *P. longicauda* in its smaller size, is the only other species known to have this structure. However this species is not examined by electron microscopy and we are not able to estimate at present whether caudate appendage is more important as a diagnostic character than the other features mentioned above or whether it should be considered of secondary value. (5) Pattern of penetration of the thylakoids into the pyrenoid matrix: At present, there are at least four types recognized of pyrenoid structure. They are as follows: 1) vertically invaded type, known in *P. longicauda* (present paper), *P. virginica* (PENNICK 1977), *P. lunata* (INOUYE *et al.* 1983) and *P. disomata* sensu NORRIS and PIENAAR (1978) (unpublished observation), 2) horizontally parallel type, known in *P. parkeae* (NORRIS and PEARSON 1975), 3) horizontally single type, known in *P. grossii* (MANTON 1965, PENNICK and CLARKE 1976) and 4) anastomose type, known in *P. amylifera* (MANTON *et al.* 1963; MANTON 1966; PENNICK 1976) and *P. tetrarhynchus* (MANTON 1968). The occurrence of these pyrenoid type is not correlated with any of the features mentioned above, although it is constant and specific in each species.

Emended description of *Pyramimonas longicauda*

Pyramimonas longicauda VAN MEEL emend. INOUYE et CHIHARA, Bull. Inst. Sc. Nat. Belg. **45**: 3. *pl.* 1, *f.* L, 1969.

Synonym: *Pyramimonas ostendensis* VAN MEEL, Bull. Inst. Sc. Nat. Belg. **45**: 2. *pl.* *f.* N, 1969.

Cells arrow-head, funnel-like or elongated obpyriform in lateral view, having 4 distinct longitudinal ridges, and with or without a posteriorly projecting caudate appendage, cruciate to square in polar view, dimensions 16-48 μm long (12.5-20.5 μm excluding caudate appendage), 10.0-22.5 μm wide. Flagella four, arising from an anteriorly located pit; chloroplast single, with four lobes widely separated at the anterior; eye-spots two, located close to each other in anterio-lateral position; pyrenoid single, located posteriorly, surrounded by two starch plates.

Scales present on flagella and cell-body. Flagellar scales of 3 types: square to pentagonal inner layer scales, ca. 40 nm each side; Limulus-shaped outer layer scales, flat, spine-tipped, 400-500 nm; hair scales, 0.8-1.2 μm long. Body scales of 3 types: square-shaped innermost layer scales, ca. 45 nm each side; large intermediate layer scales made up of square-shaped baseplate, 0.6-1.0 μm on each side and basket-shaped superstructure; large outermost layer scales box-like, consisting of base-plate, 1.0-1.2 μm on each side, and four sides made up of rod-like elements.

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井上 勲・堀 輝三・千原光雄: *Pyramimonas longicauda* (プラシノ藻) の観察と分類

尾状突起をもつ *Pyramimonas* を分離・培養し，観察を行った。クローン培養の結果，この藻は形態の著しい可塑性を示し，典型として次の二つの細胞形態をとることが明らかになった。(1) 細胞は矢羽形で頂面観は十字形，(2) 細胞は典型的なピラミモナス形で頂面観は丸みを帯びた四辺形。これら二型はそれぞれ VAN MEEL (1969) により記載された尾状突起をもつ二種 *P. ostendensis* と *P. longicauda* に酷似しており，この二種の相違は同一種内の形態変異と結論された。これらを同種と認めて識別形質の修正を行い，*P. longicauda* を正名として指定した。

微細構造上，*P. longicauda* は以下の特徴を有する。(1) 体長中層鱗片は正方形の底盤とカゴ状上部構造からなる。(2) 体表外層鱗片は箱状。(3) トリコシストをもたない。(4) 鞭毛基部の配列は菱形。(5) 鱗片貯蔵胞は未発達。(6) ピレノイドは前方からチラコイドの侵入をうける。これらの特徴の識別形質としての有効性についても論議した。(305 茨城県新治郡桜村天王台 1-1-1，筑波大学生物科学系)