J. mar. biol. Ass. U.K. (1969) 49, 129–139
Printed in Great Britain

A NEW PUNCTATE SPECIES OF *HALOSPHAERA*

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(With 16 Figures in Text and on Plate I)

The new species *Halosphaera parkeae* (Prasinophyceae) is described from material collected in the western English Channel. The microscopical structure of the outer wall of the non-motile phase is described and two types of punctation are demonstrated. A general account of the cytology of the mature non-motile phase and of the motile cell is given. Electron micrographs of the scales of the motile cell are compared with those of other species of the genus where known. Buoyancy, size and reproduction are discussed and a number of new taxonomic characters emphasized. The occurence in the same areas of a second type very similar but smaller in size is recorded and the authors have named this form *Halosphaera parkeae* forma *minuta*.

INTRODUCTION

In their paper on three species of *Halosphaera* Schmitz (Prasinophyceae) Parke & den Hartog-Adams (1965) described a new species, *H. russellii*, and compared it with *H. viridis* Schmitz and *H. minor* Ostenfeld. On 24 April 1968 in the western English Channel, under conditions of extreme calm, large green patches of *Halosphaera* were observed on the surface of the sea. The salinity of the water at this position (49° 20′ N, 5° 55′ W) was 35·25‰ and the surface temperature 11·2 °C. Although the individual patches were relatively small they occurred quite frequently in the area through which the ship was passing. They could also be spotted from a considerable distance, as they gave an oily appearance to the water surface. A detailed study of the *Halosphaera* producing these patches showed that most of the material was of a species previously recorded in the Western Approaches but not yet described. We now give it the name *Halosphaera parkeae* sp.nov. A further cruise was made 12 days later to collect more material but the weather had deteriorated and no *Halosphaera* patches were present on the surface. However, additional material of the same species was obtained from tow-net samples taken at 5 and 10 m depth. These samples also contained good numbers of a smaller

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Halosphaera, which after careful analysis we have decided to consider as a form of *Halosphaera parkeae*. We name it *Halosphaera parkeae* forma *minuta* forma nov.

DESCRIPTION

Halosphaera parkeae sp.nov. forma **parkeae**

Cellula in statu coccoïde (Fig. 7) sphaerica, matura 400–550 μ diam., membrana distromatica induta. Stratum exterius tenax, elasticum, regulariter punctatum, punctis in cellula viva haud conspicuis, in membrana vacua visibilibus, aliis maioribus 20–60 μ distantibus, quoque e facie exteriore membranae vacuae collapsae viso porum centralem 0·8 μ diam. areamque radiatim striatam ad 5 μ diam. (Fig. 9) exhibente, oblique viso conum eminentem costatum perforatum ostendente, aliis minoribus circiter 1 μ distantibus, 0·5 μ diam. (Fig. 9), membranam quasi rugulosam reddentibus. Stratum interius (Fig. 10) tenue, valde elasticum, variis substantiis dissolutis vario modo permeabile. Chromatophora (Fig. 1–3) pallide viridia, forma irregularia, ad 9 μ diam., testas amyleas multas praebentia (Fig. 2), pyrenoidibus tamen nullis observatis, sparse distributa, filis protoplasmaticis manifestis inter se connexa, cellula ita reticulata apparente (Fig. 1, 11). Corpora lipoïda valde refringentia numerosa, 1–5, mediis 2·5 μ diam. (Fig. 1, 11). Rosulae 25–30 μ diam., primum stelliformes, deinde rotundatae, 512 in quaque cellula (Fig. 3, 7).

Cellula in statu erratico (Fig. 4–6, 12) 10–16 μ longa, dimidium vel duas partes lata, obovata, postice paulum acuta, antice in quattuor lobos subacutos producta costas longitudinales cellulae terminantes, foveam centralem cingentes unde quattuor flagella aequalia cellula sesqui longiora. Chromatophorum pallide viride, anulum parietalem formans juxta costas in quattuor lobos anticos et in quattuor posticos ultimam partem cellulae non attingentes productum, ad bases loborum anticorum quattuor pyrenoïda fovens elliptica, 2 μ longa, testis amyleis circumdata. Nucleus 4 μ diam., ante mediam cellulam superficiei approprinquatus. Vacuolum posticum, 4–5 μ diam. Stigma ovale, complanatum, 1–2 μ longum. Corpora mucifera superficialia, ad ultimam partem posteriorem praesertim crebra.

Cellulae coccoïdes ante Fretum Oceani mensibus (Januario) Februario–Augusto, in ipso Freto prope Plymouth Angliae mensibus Majo–Julio observatae, rosulis Aprili–Junio frequentioribus. Planta die 24. Aprilis 1968 lat. bor. 49° 20′, long. occ. 5° 55′ lecta Fig. 1–14 delineata, Fig. 4 et 7 holotypum efficientibus speciei novae ex Doctore Mary Parke nominatae phycologa laboratorii societatis Marine Biological Association of the United Kingdom in Plymouth siti.

Non-motile phase (Fig. 7) spherical, 400–550 μ in diameter when mature. Wall of two layers, outer wall tough, elastic, with evenly distributed punctae; punctae of two types, inconspicuous on living cell, visible on empty wall (measurements on empty collapsed walls), larger punctae, 20–60 μ apart, in surface view showing central pores (0·8 μ), each with surrounding stellate ornamentation (up to 5 μ across) (Fig. 9), in oblique view appearing as perforated protruding ribbed cones; smaller punctae about 1 μ apart, measuring 0·5 μ (Fig. 9), giving wall a rugose appearance. Inner wall thin, very elastic (Fig. 10) and showing features of differential permeability. Chloroplasts (Figs. 1–3) pale green, irregularly shaped, up to 9 μ across, each with many starch shells (Fig. 2), pyrenoids not observed. Chloroplasts thinly distributed, connected by obvious protoplasmic threads giving whole cell a 'lacy' appearance (Figs. 1, 11). Large numbers of highly refractive lipoid bodies present 1–5 μ in diameter, average diameter 2·5 μ (Figs. 1, 11). Rosettes 25–30 μ in diameter, stellate in early stages, rounded, later 512 rosettes per non-motile phase (Figs. 3, 7).

Cells of motile phase (Figs. 4–6, 12) 10–16 μ long, ½–⅝ as broad as long. Body obovate with slightly pointed posterior pole and four bluntly pointed lobes at anterior pole, extending down the body as costae. Anterior body lobes surrounding a depression from which four equal flagella arise; flagella 1½ times the body length. Chloroplast pale green, annular parietal with four lobes extending forwards and backwards along the costae but not reaching posterior pole, pyrenoids four, elliptical, 2 μ long, in chloroplast at base of anterior lobes, surrounded by starch shells. Nucleus 4 μ in diameter excentrically and somewhat anteriorly placed. Vacuole 4–5 μ in diameter posteriorly placed; oval, flattened stigma, 1–2 μ long, present. Muciferous bodies periferal, especially abundant near posterior pole.

Recorded occurrence of non-motile phase, Western Approaches (January), February–August, Plymouth area May–July. Rosettes most abundant April–June. Collected in N. Atlantic at 49° 20′ N, 5° 55′ W., 24 April 1968. Illustrated in Figs. 1–14, of which Figs. 4 and 7 are the holotype.

Named after Dr Mary Parke, phycologist at the Plymouth Laboratory of the Marine Biological Association of the United Kingdom.

Halosphaera parkeae forma **minuta** forma nov.

A forma parkeae cellula coccoïde matura minore, 200–250 μ diam., 128–256 modo rosulas 20–25 μ diam. praebente diversa (Fig. 15, formae holotypus).

Cellulae coccoïdes ante Fretum Oceani mensibus Januario–Julio, in ipso Freto prope Plymouth Angliae mensibus Martio–Majo et Septembri–Novembri observatae, rosulis Martio–Junio frequentioribus.

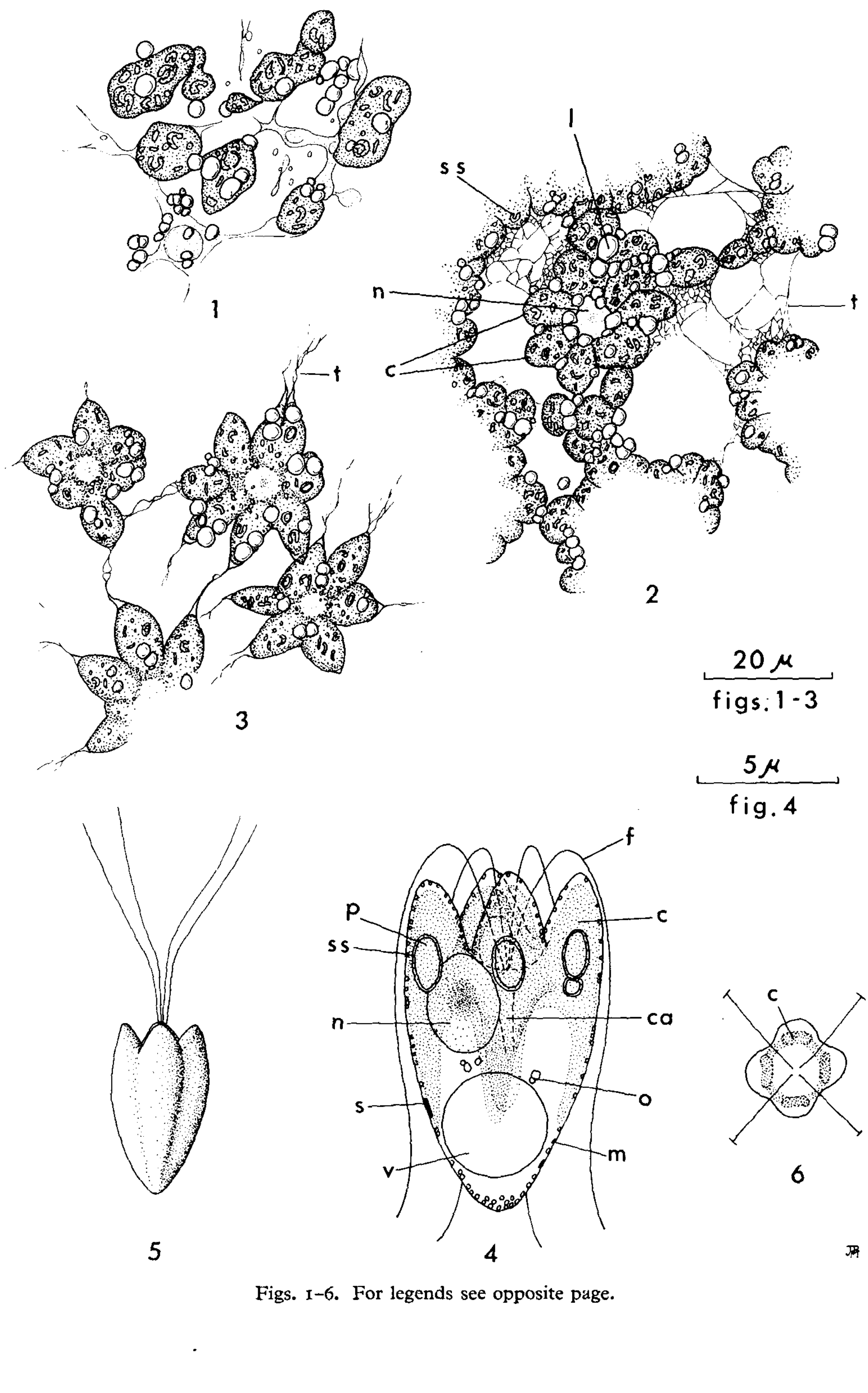
Non-motile and motile phase as *Halosphaera parkeae* forma *parkeae* except in the smaller size of the non-motile phase when mature; non-motile phase 200–250 μ in diameter, producing only 128–256 rosettes, each 20–25 μ in diameter.

Recorded occurrence of non-motile phase, Western Approaches January–July, Plymouth area March–May and September–November. Rosettes most abundant March–June. Figure 15 is the holotype.

In considering this new species the similarities and differences between it and the other three species recorded for the area will be emphasized. Dr Parke has occasionally observed material of this species over the last few years and has always referred to it as 'Lacy *Halosphaera*'. This is because in the immature non-motile phase the chloroplasts are rather scattered but are linked by conspicuous protoplasmic threads thus giving the sphere its characteristic lacy appearance. The other three species, *H. viridis*, *H. minor* and *H. russellii*, have a more compact appearance.

Non-motile phase

H. parkeae reaches maturity at 400–550 μ, which is much the same size as *H. russellii* but smaller than *H. viridis* and larger than *H. minor*. The size composition of the population sampled on 24 April 1968 is illustrated in the histograms (Fig. 16). The population is divided into mature ('rosette stage'—the chloroplasts gather about the nuclei leading to the formation of units termed rosettes by Parke & den Hartog-Adams, 1965) and immature ('pre-rosette stage') cells. As with all *Halosphaera* species, the non-motile phase of



Figs. 1–6. For legends see opposite page.

H. parkeae has a double wall. The outer wall is punctate as in *H. russellii* (the only other punctate species known off South-West Britain) but in the latter species the ornamentations are readily visible in the living cell even at low magnification while those of *H. parkeae* can only just be seen on the living cell at the highest magnification. When the cell is stained with Lugol's reagent they can, however, be seen on the outer wall, where they appear as white spots. This we consider to indicate that they are probably perforations. The distribution of punctations is not so regular as in *H. russellii* but the punctae are approximately equidistant. The punctations are most readily seen on collapsed empty walls when the internal pressure is released and the wall is no longer stretched (Fig. 8). With high-power phase microscopy the punctations appear, in oblique view, as volcano-like protuberances (where the crater is probably a perforation) with radiating ridges, the nature of which is still to be examined with the electron microscope. The star-like aspect of the ridges around the punctations, when viewed from above (Fig. 9), is characteristic. It is more obvious on some walls than on others. In addition the surface between the large pores is finely punctate, giving the whole surface a rugose appearance (Fig. 9). The fine structure of these punctations has still to be elucidated. All the measurements of punctations have been made on collapsed empty walls.

The outer wall of *H. parkeae* appears, from the way it collapses, to be thinner than in the other three species. In common with these three species the outer wall is resilient and stains readily with Lugol's reagent (orange-yellow) and the Sudan lipoid stains. The inner wall, as in the other species, is quite different from the outer wall; it is much thinner, much more elastic and has no characteristic markings. It is permeable to iodine and weakly stained by it, but impermeable to the Sudan stains so that any lipoid material inside the intact inner wall cannot be demonstrated. But if this wall is ruptured the lightly refractive bodies, previously called reservoirs in other species by Parke & den Hartog-Adams (1965), are readily stained by lipoid dyes (Fig. 10). Norris (1961) has reported similar difficulties when trying to use Mayer's acid haemalum. These differences in reaction to dyes give some indication as to the different chemical structure of the two walls.

Figs. 1–3. Three stages in the maturation of the non-motile phase of *Halosphaera parkeae*. (1) Cytoplasmic inclusions in immature stage of the non-motile phase. (2) Chloroplasts collecting around nuclei at the beginning of the rosette formation. (3) Later stage in maturation (rosettes separating).

Fig. 4. Motile cell of *Halosphaera parkeae* with flagella in position for swimming with flagellar pole forwards.

Fig. 5. Motile cell with flagella in position for swimming with flagellar pole behind.

Fig. 6. Motile cell apical view.

c, Chloroplast; *ca*, area stained with neutral red between apical depression and vacuole; *f*, flagellum; *l*, lipoid bodies; *m*, muciferous organelles; *n*, nucleus; *o*, oil droplets; *p*, pyrenoids; *s*, stigma; *ss*, starch shells; *t*, protoplasmic trabeculae; *v*, vacuole.

The cytoplasmic contents are parietal and similar to those described for the other species by Parke & den Hartog-Adams (1965). The irregular chloroplasts contain numerous starch shells which, when stained with iodine, take up the reddish purple colour characteristic of prasinophycean starch. The division of the original single nucleus and the further aggregation of cytoplasmic contents about each of the resultant nuclei follows essentially the same pattern as that described by Parke & den Hartog-Adams (1965) for other species of *Halosphaera*. During the aggregation of the cell-contents, the protoplasmic trabeculae between the chloroplasts become more evident and

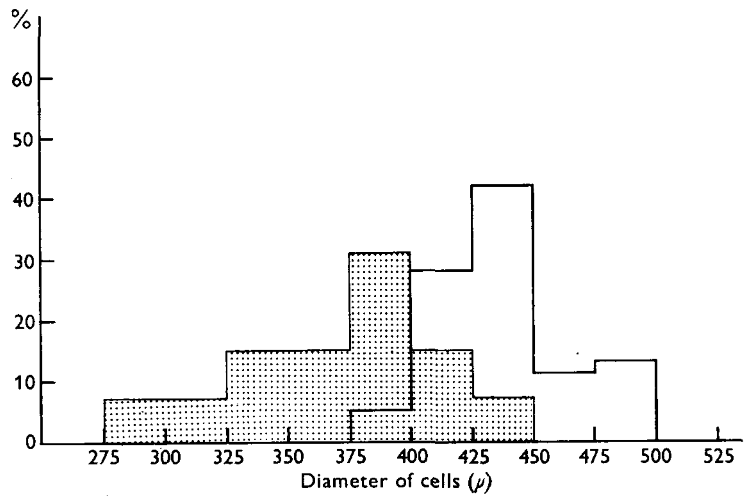


Fig. 16. Histograms of size distribution of the population of the non-motile cells of *Halosphaera parkeae* sampled on 24 April 1968. Stippled, prerosette stage; blank, rosette stage.

the lacy appearance is more pronounced (Figs. 1–3). In forma *parkeae* the mature non-motile phase has 512 rosettes whereas in forma *minuta* (Fig. 15) there are 128–256. When the rosettes are fully developed they divide up to give the quadriflagellate motile cells. At this stage the inner envelope swells and bursts the outer wall, from which it escapes with its contents still dividing; later on the thin envelope also bursts and releases the matured motile cells (see also Parke & den Hartog-Adams, 1965). As the outer wall of *H. parkeae* is thinner than in other species it does not take up a characteristic shape when empty.

Motile phase

The motile cells of *H. parkeae* are illustrated in Figs. 4–6 and are drawn in such a way as to be comparable with the illustrations for the three species given by Parke & den Hartog-Adams (1965). Most of the posterior part of the motile cell is occupied by a large organelle which we believe to be a vacuole as it stains readily with neutral red. This vacuole does not take up lipoid dyes

TABLE 1. COMPARATIVE CHARACTERS OF *HALOSPHAERA* SPECIES

	Halosphaera viridis	*Halosphaera minor*	*Halosphaera russellii*	*Halosphaera parkeae* f. parkeae	*Halosphaera parkeae* f. minuta
Non-Motile phase					
Size at maturity (μ)	400–800	190–235	300–500	400–550	200–250
Outer wall	Smooth-pleats in a characteristic manner when cast	Smooth-folds like a deflated football bladder when cast	Punctate. Readily visible in living cell. 20–25 μ apart. Folds like a deflated football bladder when cast	Punctate. Not readily visible on living cell. Two types of punctae seen on empty wall. No definite form of collapse.	Punctate. Not readily visible on living cell. Two types of punctae seen on empty wall. No definite form of collapse.
Rosettes					
Number	256 or 512	64	128 or 256	512	128 or 256
Shape	Round to oval	Round	Round to oval	Round	Round
Margin	Smooth	Fairly smooth	Lobed	Lobed to round	Lobed to round
Size (μ)	30–50	30–45	15–20	25–30	20–25
Chloroplasts	Pale green, up to 8 μ	Deepish green, spindle-shaped or angled, 3–5 μ	Yellowish green rounded oval plates, 3–6 μ	Pale green, irregular, up to 9 μ	Pale green irregular, up to 9 μ
Pyrenoids and starch sheaths	3–6 μ not conspicuous	2–3 μ, not conspicuous	3–5 μ, conspicuous	Numerous small starch shells, pyrenoids not observed	Numerous small starch shell, pyrenoids not observed
Lipoid bodies	Not conspicuous	Conspicuous	Not very conspicuous	Conspicuous	Conspicuous
Recorded occurrence in West Channel and Bay of Biscay	November–July	Throughout most of year	Throughout most of year	January–August	Throughout most of year
Recorded mature in these areas	February–July	January–July	March–July	February–June	February–July
Motile phase					
Size (μ)	20–28	14–28	12–22·5	10–16	10–16
Body					
Anterior lobes	Short and slightly pointed	With flattened extremities	Very pointed	Short and slightly pointed	Short and slightly pointed
Posterior pole	Rounded or slightly pointed	Rounded	Sharply pointed	Slightly pointed	Slightly pointed
Apical depression	Rather narrow and cylindrical in shape	Wide-basin shape	Shallow-basin shape	Rounded and basin-shaped	Rounded and basin-shaped
Flagella length	2 × body length	$1\frac{1}{2}$–2 × body length	2 × body length	$1\frac{1}{2}$ × body length	$1\frac{1}{2}$ × body length
Chloroplasts	Pale green, lining greater part of periplast and appearing granular	Deepish green filling apical body lobes and extending posteriorly as 4 long rather narrow lobes	Pale yellowish green, very delicate, not filling apical body lobes and extending posteriorly as 4 very narrow lobes	Pale green, filling apical body lobes and extending posteriorly as 4 rather narrow lobes	Pale green, filling lobes and extending posteriorly as 4 rather narrow lobes
Vacuole (?)	3–6 μ, sometimes obscure	5–10 μ, conspicuous	3–5 μ, usually visible	4–5 μ, conspicuous	4–5 μ, conspicuous
Body scales					
Lower layer		Small squares	Small squares	Small squares	Small squares
Upper layer		Large lacy squares and circles	Only large lacy squares recorded	Large lacy circles and new oval type	Large lacy circles and new oval type
Flagellum scales					
Lower layer		Small circles	Small circles	Small circles	Small circles
Upper layer		Oval spined scales	Oval spined scales	Oval spined scales	Oval spined scales

and probably has no connexion with the lipoid bodies of the non-motile phase. Neutral red also stains an area between the vacuole and the apical depression (Fig. 4, *ca*). The evidence of Parke & Adams (1961) that graphite entered this vacuole suggests that at some time it must have an opening to the outside, although Manton, Oates & Parke (1963) could not find any canal.

The fine structure of the motile cells of other species of *Halosphaera* has been examined with the electron microscope by Manton *et al.* (1963) who showed that both the body and flagella of the motile cells were covered with scales. We have carried out a few external examinations of this new species to determine the scale types present. These are illustrated in Fig. 13–14 and should be compared with those of *H. russellii* (Plymouth no. 247) and *H. minor* (Plymouth no. 205) (Manton *et al.* 1963). The flagellar scales and the small underlayer scales of body and flagellum are similar in the three species. However, we find differences in the body scales, the main one being that *H. parkeae* does not have the square scales shown by Manton *et al.* (1963), plate III, fig. 8 and plate IV, fig. 12, but has the rounded ones similar to those shown in plate IV, fig. 12. In addition, *H. parkeae* has a new elliptical type of scale not previously recorded for *Halosphaera* species (Fig. 14).

As a further comparison we have modified the table of characters given by Parke & den Hartog-Adams (1965) and extended it to include the two new forms described in this paper (Table 1).

DISCUSSION

The finding of a new species of *Halosphaera* in the western Channel leads us to consider some facts that may be of interest for future research on this still little-known genus.

Either neustonic—due to abundant storage of lipoid material—or merely planktonic, the cells of *Halosphaera* have escaped many researches restricted to only one type of biocoenose. The reason for variations in lipoid content is a problem for the experimental physiologist, and further investigation depends upon an improvement in our ability to keep cells in culture. It is known from the work of Spoehr & Milner (1949) that lipoid production is stimulated by light in some algal classes. Without asserting that such is the case with *Halosphaera*, we believe that further research into metabolic mechanisms in the Prasinophyceae is needed. The persistence of cells at great depth in a specific water body in the Atlantic Ocean (Yashnov, 1965) may be partly due to an adjustment in buoyancy (but their survival well below the euphotic layer still remains a puzzle). On the other hand it has been demonstrated that many algae accumulate lipoid material as a response to a nitrogen deficiency in the medium. The exhaustion of nitrogen in the euphotic layer of the sea during the late spring and summer could then account for the accumulation of lipoid observed in *Halosphaera*.

The occurrence of two forms differing only in the size at which they mature focuses attention on the problem of size variation in *Halosphaera*. Sexual reproduction could account for this difference but it has never been proved beyond doubt that this occurs in the Prasinophyceae (McLachlan & Parke, 1967). Rayns (1963) has said for *Halosphaera* that 'all isolations had nuclei with the same chromosome number. All divisions in both phases were mitotic except for a few instances where possible meiotic configurations were seen'. Gorbunova (1961) has reported fusion phenomena in *Asteromonas gracilis* (Peterfi & Manton, 1968, consider this was abnormal division). However, both of these observations still require further investigation. Another possibility is that different environmental conditions have induced different growth rates in two different populations before climatic factors led to the waters mixing. Once again, there is no evidence of such a mechanism. Further, it may be that here we have two races—or forms—of one species differing only in the size at which the nucleus in the non-motile phase begins to divide up and hence bring about maturity. We believe that this problem cannot be solved without a world-wide investigation of the genus. Thus, until more evidence is available we have decided to consider the two types under investigation here as forms of one species.

The study of *Halosphaera parkeae* has allowed us to emphasize a number of new characters that may prove useful in future diagnoses of *Halosphaera* species. The ornamentation of the outer wall of the non-motile phase is a major character and probably shows little variation. This feature may be discrete and thus requires a careful examination. The puncturing of the non-motile cell and the expulsion of contents by pressure on the coverslip above the cell is a simple and quick operation. Equally important are the types of scales found in the outer layer of the body of the motile cell. Finally, presence or apparent absence of pyrenoids, shape and number of starch shells in the chloroplasts and abundance or otherwise of lipoid material in the mature non-motile cell may give valuable information. However, as metabolic products may vary according to environmental factors, special caution is required in the interpretation of such results.

We wish to express our grateful thanks to Dr M. Parke for her guidance and encouragement and for kindly allowing us to use her records of this new species, and also to Dr T. Christensen for translating the diagnosis into Latin.

We are indebted to the captains and crews of the Laboratory research vessels for help in collecting material, to Miss R. Jowett for help with the electron microscopy and Miss J. Hearn and Mr D. Harbour for technical assistance. One of us (J.P.M) also thanks the Director of the Plymouth Laboratory for providing research facilities and U.N.E.S.C.O. for the fellowship making this work possible.

RÉSUMÉ

Halosphaera parkeae nov.sp. (Prasinophycées) trouvée dans la Manche occidentale, est décrite dans cet article. Le cyste (ici appelé phase non mobile) a sa membrane extérieure régulièrement ponctuée (deux types de ponctuation), ce qui n'apparaît néanmoins que sur la cellule vide ou rompue. Au point de vue cytologique, au cours de la formation du stade coenocytique, le cyste est caractérisé par un fin réseau de trabécules cytoplasmiques qui emprisonne les organites. La nature lipidique de corpuscules réfringents jusqu'ici connus comme 'réservoirs' est démontrée en même temps que les propriétés de perméabilité très différentes des membranes externe et interne. Les zoospores sont également étudiées et comparées avec celles des autres espèces, notamment en ce qui concerne la structure fine des écailles qui couvrent les flagelles et le corps des cellules. Une autre forme de cette nouvelle espèce, *Halosphaera parkeae* forma *minuta*, est également présente dans l'aire étudiée.

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EXPLANATION OF PLATE I

Fig. 7. Three non-motile cells of *Halosphaera parkeae*, one immature pre-rosette stage, part of another and part of a cell in rosette stage. ×90.

Fig. 8. Empty outer wall flattened under coverslip and showing the coarse punctae. Phase-contrast. ×115.

Fig. 9. Single stellate punctation and fine punctations on outer wall. Phase contrast. ×1150.

Fig. 10. Cell collapsed by pressure on the coverslip and stained with Sudan blue. The outer wall and the lipoid bodies inside the ruptured inner-wall take up the dye. The inner wall remains unstained.

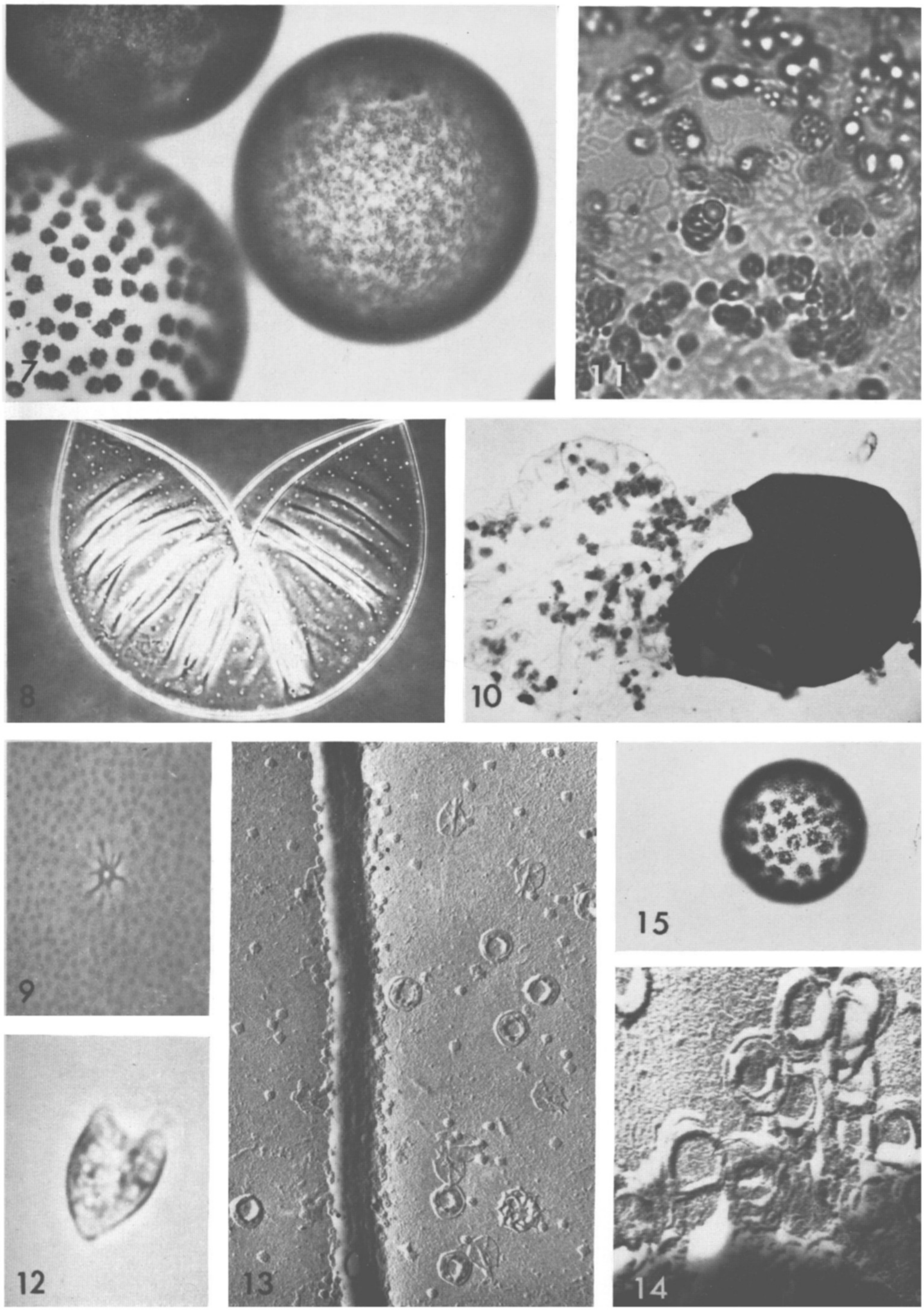

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Fig. 11. Detail of living immature cell, showing chloroplasts with numerous starch shells and highly refractive lipoid bodies. The protoplasmic trabeculae between the chloroplasts are conspicuous. × 700.

Fig. 12. Single motile cell. × 1600.

Fig. 13. Part of a flagellum surrounded by detached body and flagellar scales. The under-layer flagellar scales are very small and circular, the upper-layer flagellar scales are lacy with a projecting ridge. The under-layer body scales are very small and square and the upper-layer body scales are of two types: wheel-like lacy scales and round-to-oval thick-rimmed scales. × 15,000.

Fig. 14. Group of the thick-rimmed oval body scales near a cell. × 37,300.

Fig. 15. Non-motile cell of *Halosphaera parkeae* forma *minuta* in rosette stage. × 90.