A species of Proboscidiella from Kalotermes (Cryptotermes) dudleyi Banks, a termite of Central America, with remarks on the oxy-monad flagellates.

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With Plates 21–24.

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I. Introduction and Historical Account.

An interesting group of Protozoa living in termites is that comprising the oxymonads, which in many ways are very different from other known flagellates. By prolongations of the anterior
ends of the bodies they may attach themselves to the lining of the intestine, but they are also able to swim about in the lumen of the canal. Having no cytostomes they ingest wood, as do many termite flagellates, through the general surface of the body.

What was probably the first member of this group to be recorded is *Microrhopalodina enflata* from *Kalotermes flavicollis* of Europe, which was described but not figured by Grassi and Foà (1911). In the usual form this organism is multinucleate, and is attached to the intestinal wall by a ‘peduncle’ or ‘neck’. When the host moults, however, the parasite is said to become free, lose the ‘neck’, and develop flagella. A fuller discussion of this genus will be given later (p. 378).

Janicki (1915) described *Oxymonas granulosa* from *Neotermes connexus* ('*Kalotermus castaneus*') of Hawaii, giving an account of mitotic division. He noticed that this organism resembled *Microrhopalodina* in several respects, but separated it generically chiefly because, in contrast to Grassi’s flagellate, it was usually uninucleate, though rarely binucleate.

In his monograph on the flagellates of termites Grassi (1917) figures flask-shaped flagellates from *N. erytraeus* and *Glyptotermes parvulus* which are undoubtedly oxymonads. He did not recognize that fact, however, but supposed them to be developmental stages of multinucleate flagellates of the family Calonymphidae.

Recently Kofoid and Swezy (1926 a, b) gave an account of three new species of *Oxymonas*, re-examined Janicki’s species, correcting his account for flagella and other structural details, and described a new multinucleate oxymonad, *Proboscidicella multinucleata*. Later in the same year a small species of *Oxymonas* was recorded from *Cryptotermes hermsi* (Kirby, 1926).

As a result of the study of the Protozoa of termites collected in 1925 in the Canal Zone and Costa Rica, as well as of several species obtained from other localities, it is possible for the
writer to make some additions to the knowledge of this group of flagellates. These studies, as well as others still unpublished, have been facilitated by material placed at my disposal by Dr. A. E. Emerson, Dr. S. F. Light, Mr. G. F. Hill, Mr. J. E. Zetek, and Dr. L. R. Cleveland. The Central American collections were made with the aid of a grant given to Dr. L. R. Cleveland by the Bache Fund of the National Academy of Sciences, and were identified by Dr. T. E. Snyder. Many of the illustrations were prepared by Miss Lisbeth Krause.

II. MATERIAL AND TECHNIQUE.

The observations on living uninucleate oxymonads which are here recorded were made on material from four species of Kalotermes s. str., two of which came from Central America and two from California. Of C. dudleyi the material at my disposal was obtained from two sources: a colony (T-234) collected by Mr. Zetek in Ancon, and one (T-239) collected from furniture in Balboa, Canal Zone. Smears from the former were prepared at the Barro Colorado Island Biological Station soon after their capture; the latter were brought to New Haven and fed for variable periods on filter paper before preparations were made.

In addition to the usual methods of preparing material, fixation in osmic vapour and use of the dark-field condenser were of much assistance. The former procedure, with subsequent staining in iron haematoxylin, facilitated observations on the flagella and blepharoplasts. Unfortunately this method was not used for Proboscidiella, but fixation in Flemming’s fluid without acetic acid gave comparable results. Staining in Delafield’s haematoxylin after fixation in Schaudinn’s fluid was very satisfactory for nuclear structure and assisted in the formation of conclusions concerning the existence of a parabasal body, for in other material on the same slides (Devescovina, Stephanonympha, and others) the parabasal was well stained.1 The dark-field condenser fitted to a mon-objective...

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1 The parabasal bodies of many flagellates in termites, including Trichomonas, Devescovina, Calonympha, and Stephanonympha...
binocular microscope proved very helpful in determination of the number and length of flagella in the uninucleate oxymonads, but this equipment was obtained too late for use with Proboscidiella. On serial sections of the intestine of C. dudleyi the flagellates could be studied in their normal relation to the intestinal wall.

III. THE UNINUCLEATE OXYMONADS.

The oxymonads have a limited distribution among termites, as they have been found only in members of one sub-family, the Kalotermitinae. In this group, however, they seem to be widespread, for an oxymonad occurs in thirty-one of the thirty-six species listed on pp. 382–8, and is not known to be absent from four of the other five. Although none has been found by the writer in Porotermes grandis, the significance of this probable exception is less because the genus Porotermes differs both structurally and in flagellate fauna from other members of the sub-family to a greater extent than these differ among themselves. In twenty-two species of these termites which the author has studied, and in six other species recorded in the literature, an oxymonad occurs which is predominantly uninucleate. In C. dudleyi this is replaced by a multinucleate form similar to P. multinucleata, and in Calcaritermes brevicollis there is, in addition to the uninucleate form, an undescribed multinucleate flagellate with an organ of attachment similar to that of Proboscidiella, but with a different form and arrangement of nuclei and body-fibres.

Observations on flagellates similar to Oxymonas from K. tabogae and K. marginipennis of Central America, and K. hubbardi and K. minor of California, were made by reflected light from the dark-field condenser. In every instance four long flagella were seen (figs. 1–9, Pl. 21). In a crushed specimen, are clearly demonstrated by staining in Delafield's haematoxylin, after fixation in Schaudinn's fluid with or without acetic acid. In the case of Metadevescovina debilis from Kalotermes hubbardi the addition of 10 per cent. acetic acid to the fixing fluid had no apparent effect on the parabasal body.
In three species of Oxymonas from South American termites, and presumably also in O. granulosa, which was re-examined, Kofoid and Swezy (1926) found six short flagella, three attached to each blepharoplast. They give this number as characteristic of the genus, stating that ‘this genus is fundamentally of the triflagellate type’. In accordance with this and other observations, the genus Oxymonas Janicki, 1915, is emended by them to include the two blepharoplasts, each connected by a rhizoplast to a centrosome on the nuclear membrane, and connected together by a semicircular filament, and the three flagella arising from each blepharoplast.

In features other than the flagella, the uninucleate oxy-monads which the writer has observed resemble those described by Kofoid and Swezy. Because of the difference in that respect, however, it may be necessary, in agreement with the procedure followed in the case of trichomonad and other flagellates, to establish another genus for the forms with four flagella. The writer is not prepared to do this without making observations on the type species of the genus Oxymonas. It is, however, desirable to consider the quadriflagellate forms for the sake of comparing them with the new species of Proboscidiella and defining the characters of the family to which the oxymonads belong.

In addition to the value of dark-field illumination for observations on the flagella, this method facilitates study of the microorganisms adhering to the bodies of the oxymonads as well as
other flagellates of termites. The possible error, which has often been made, of confusing those organisms with flagella is thus eliminated, for their appearance and movements, when observed in this manner, are seen to be very different from those of flagella. Most of them are spiral forms, probably spirochaetes (Cleveland, 1928). By feeding the termites for a period of about ten days on filter paper soaked in 5 per cent. acid fuchsin, as recommended by Cleveland (1928), the spirochaetes may be caused to disappear from the bodies of the flagellates, as well as from the intestine of the termite. After this method had been used upon the oxymonad from K. hubbardi, rod-like forms, which had not been noticed on untreated flagellates, were found to be present.

The abundance of micro-organisms on the bodies of different individuals is, of course, very variable. The numbers vary on some species from a condition in which they cover both the body proper and the organ of attachment, to one in which there are very few or none at all. But it is possible, nevertheless, in some cases, to use the presence and abundance of certain types of micro-organisms as a specific characteristic. Thus on the oxymonad from K. hubbardi there are usually some, but not many, spirochaetes, while on that from K. panamae every individual has a dense coat of those organisms. O. pediculosa, according to Kofoid and Swezy, has a similarly large number. This point is admirably illustrated by Metaevescovina debilis from K. hubbardi, though that is not an oxymonad. On every individual of this species there are, normally, large numbers of spirochaetes, which are shorter and stouter than those on Oxymonas, forming a dense covering which has been mistaken for a coat of cilia. By feeding the host on acid fuchsin all these may be removed. On various species of uninucleate oxymonads, spirochaetes of one type, a long, narrow, much spiralled form, have been seen. As will be discussed later, this is replaced on the new species of Probosciidiella by a short, rod-like micro-organism, though longer forms are apparently present on the type species of that genus.

The above remarks on uninucleate oxymonads are included
here chiefly for comparative purposes. A detailed cytological study of the structure and mitotic division, for which material from several species is available, may be expected to clarify our knowledge of the morphology and life-history of these interesting flagellates.

IV. Proboscidiella kofoidi, sp. nov.

A multinucleate oxymonad was described by Kofoid and Swezy (1926b) from Planocryptotermes nocens Light, a termite of the Philippine Islands, under the name of P. multinucleata. In C. dudleyi Banks, a termite which occurs in the Canal Zone and which, like Pl. nocens, lives in dry wood and damages furniture and woodwork, the writer found a multinucleate flagellate very similar to it, yet sufficiently distinct to be assigned to a new species. In recognition of the work of Dr. C. A. Kofoid on this genus, it may appropriately be named P. kofoidi. The two flagellates correspond closely in most characteristics except the number and size of flagella and the arrangement of blepharoplasts in each unit. While in the type species there are described three very short flagella associated with each nucleus, each mastigont¹ of P. kofoidi possesses four long flagella.

1. Morphology and Behaviour.

A characteristic structure of Proboscidiella, as well as of Oxymonas, is the organelle of attachment called by Kofoid and Swezy a proboscis, but perhaps more appropriately termed a rostellum,² which, because of its great variability in length, is

¹ The term karyomastigont was used by Janicki for the complex in Stephanonympha and Calonympha consisting of one nucleus with the surrounding portion of the cytoplasm, the blepharoplast, the parabasal apparatus, the axial filament, and the flagella emerging from that blepharoplast. It is synonymous with the single neuromotor system with its associated nucleus, as used by Kofoid, except that this does not include the portion of cytoplasm. When the nucleus is lacking (in Calonympha) the term akaryomastigont is applied to the remaining structures, while mastigont may be used without reference to presence or absence of the nucleus, thus including both of the other terms.

² As used in metazoan morphology the term proboscis is applicable to
believed by them to be highly contractile. In the hind-gut of the termite flagellates may be closely crowded together, attached to the wall by these organelles (fig. 10, Pl. 22). Since in C. dulleyi, as in other termites, there is a chitinous intima lining this part of the intestine, the expanded ends of the rostella are not applied directly to the epithelial cells.

The intestinal faunas of many termites of the host species brought to New Haven and examined while living were found to consist of several species of flagellates, including Stephanonympha, Devescovina, a five-flagellated trichomonad and smaller forms, in addition to forms of Proboscidiella both with and without rostella. In shape and size the latter forms of Proboscidiella, although very variable, resembled Stephanonympha (36–96×31–78 microns). The flagella, which exceeded in length those of Stephanonympha, were all directed backward over the body and were in active motion, slowly propelling the organism forward. The area anterior to the nuclei, where, in other individuals, an organelle of attachment may be developed, was evenly rounded and clear. In the cytoplasm of these motile individuals were numerous spherical inclusions and particles of wood, the latter sometimes so large that the bodies were distorted to accommodate them. Rostellate forms were also abundant, though less so in this material than the motile forms. Although actively moving flagella were present on some of the rostellate individuals, others lacked those structures. The latter observation agrees to some extent with that made by Grassi on Microrhopalodina, that the attached individuals lacked flagella.

The body is usually broadly ovoidal or pyriform, narrowing an organ, usually tubular, developed in connexion with the head if not the mouth. The numerous structures grouped under this name are of diverse natures, many functioning in relation with feeding, while others have different uses, but not that of attachment. It is somewhat misleading to use this term for a structure of a unicellular organism which is not tubular nor associated in any way with feeding, but functions for attachment. These implications are avoided by use of the term rostellum, which, besides its use in botany, is applied to median, imperforate, more or less retractile organs of attachment on the scolices of cestodes.
towards the anterior end, from which the rostellum may be prolonged (figs. 14, 16 a, 18, Pl. 22). In a hundred individuals preserved on slides the length, exclusive of the rostellum, ranged from 23 to 165, averaging 66 microns, and the width at the broadest part of the body from 12 to 100, averaging 46 microns. Thus the length of P. kofoidi is similar to that of those individuals of P. multinucleata measured by Kofoid and Swezy, which ranged from 25 to 160 and averaged (in sixteen cases) 72 microns. On slides made from another colony (T-234) the average size was smaller, 50 x 38 microns.

On flagellates attached to the intestinal wall by the ends of the rostella, those organelles are generally relatively short and broad, though some are longer than in the individuals selected for illustration (fig. 10, Pl. 22). The end is broadly expanded and often is concave. On smears, however, the rostella are commonly longer, ranging up to 299 microns, which in this case was nearly four times the length of the body, 77 microns. Great lengths are infrequent, the usual size being from about 10 to 120, with an average in a hundred cases of 66 microns. While often the ends of the rostella are enlarged (fig. 16 a, 18; Pl. 22), frequently they are pointed or truncate (fig. 11, Pl. 22). The organelles may become broken off or detached from the flagellates, as evidenced by the fact that many isolated rostella were found on smears. It is possible, then, that some of those forms lacking rostella have not retracted the process, but it has been detached. In the rostellum there are a great many fibres, prolonged from the fibrillar system of the body (fig. 24, Pl. 23).

While oxymonads described or observed in twenty-eight species of Kalotermitinae are uninucleate, with occasional binucleate and rarely multinucleate stages, the two members of the genus Proboscidiella are predominantly multinucleate. In P. multinucleata uninucleate stages have been described, but the writer has found none in P. kofoidi. The smallest number of nuclei in several thousand individuals of the latter species was two, the largest number twenty-six (fig. 33, Pl. 24). In the latter instance the nuclei had separated into two groups of seven and nineteen, and binary fission had been proceeding.
Numbers above eleven are, however, infrequent. Though every count from two to nineteen, seldom more, occurs, eight is the most common number. This is borne out by records presented in the accompanying table from three hundred individuals on twelve slides. Of these sixty-five, which is by far the highest single number, had eight nuclei; the median number is eight and the average number in the whole group, disregarding the two exceptional cases of twenty-two and twenty-six, is 8.04.

**Frequency in Number of Nuclei in 300 Individuals.**

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<th>Number</th>
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<tr>
<td>2 - 4</td>
<td>12 - 7</td>
</tr>
<tr>
<td>3 - 7</td>
<td>13 - 6</td>
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<tr>
<td>4 - 18</td>
<td>14 - 5</td>
</tr>
<tr>
<td>5 - 24</td>
<td>15 - 1</td>
</tr>
<tr>
<td>6 - 42</td>
<td>16 - 7</td>
</tr>
<tr>
<td>7 - 39</td>
<td>17 - 3</td>
</tr>
<tr>
<td>8 - 65</td>
<td>18 - 2</td>
</tr>
<tr>
<td>9 - 27</td>
<td>19 - 2</td>
</tr>
<tr>
<td>10 - 20</td>
<td>22 - 1</td>
</tr>
<tr>
<td>11 - 19</td>
<td>26 - 1</td>
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On smears fixed in the Canal Zone soon after the termites of colony T-234 were secured, the bodies of Proboscidiella were almost without exception crowded to the base of the rostellum with yellow-brown spherules, some of which occurred among the blepharoplasts and fibrils anterior to the nuclei (fig. 16 b, Pl. 22). These spherules measured from 1 to 5, most commonly between 3 and 4 microns in diameter, and each was enclosed in a clear area, apparently a vacuole. While most of them were quite spherical in form, many were somewhat irregular in outline (fig. 17, Pl. 22). Sometimes these latter were irregularly ovoidal, in some there was a flattening or even a depression at one side, and in a few cases the globules were as irregular in outline as starch grains. The interior was not uniform in appearance, but seemed to be filled with a few large or many small vacuoles, and sometimes to contain also a few granules. When the body is ruptured these globules may remain intact after release.

In termites of another colony (T-239) which were brought to New Haven and fed for several days on filter paper, the cytoplasmic inclusions of Proboscidiella were not the same
PROBOSCIDIELLA FROM KALOTERMES 365

(fig. 11, Pl. 22; fig. 25, Pl. 23). There were fewer and smaller spherules, which did not have the same yellow-brown colour. They were usually not stained, but in material fixed in Flemming’s fluid there were among them some, similar in outline to the others, which stained deeply with iron haematoxylin, as well as some with a deeply staining shell and inner granules (fig. 20, Pl. 23). Without doubt the filter-paper feeding had altered the cytoplasmic inclusions, so that the normal situation is not presented by flagellates from hosts which had been thus treated.

Spherules similar to those of this species of Proboscidiella are abundant in O. granulosa and occasionally, at least, occur in P. multinucleata, and in some species of Calonympha and Stephanonympha. In O. pediculosa Kofoid and Swezy found in many individuals large, spherical granules which stained deeply. Janicki suggests that in O. granulosa the spherules may be derived directly from the particles of wood, which acquire a rounded form. The facts which are known all point to the conclusion that they are derived from the ingested wood, perhaps as an extracted substance. Their lack of uniformity in internal structure makes it unlikely that they are fluid reserve products.

Among the spherules, in flagellates from normally fed termites, are small wood particles, the cytoplasmic fibres, often large fragments of wood, and tubular structures of variable thickness and length within which spherules may be enclosed. In a specimen the hosts of which had been fed upon filter paper for six days, there was, at the end of the bundle of axostyles (fig. 15, Pl. 22) a curious tubular structure of different nature. The tube was stained with iron haematoxylin, and thus is comparable with similar but shorter tubes in some other specimens (fig. 11, Pl. 22). The writer has been unable to form an opinion as to the nature of these structures. They are similar to certain cytoplasmic inclusions in P. multinucleata, which Kofoid has suggested may be ‘vestigial sleeves’ handed down from an Oxymonas-like ancestor.

A narrow zone of ectoplasm is distinct in some (fig. 11, Pl. 22) but not in all specimens. This seems to be alveolar in nature, as
many fine lines, which are probably alveolar walls, traverse it. Inwardly the ectoplasmic layer, in which no cytoplasmic inclusions occur, is distinct from the endoplasm, and outwardly it is bounded by a thin pellicle.

Flagellates have been found in which there is a broad layer of granular protoplasm surrounding the body and, in some cases, partly covering the rostellum. When this substance covers an individual which lacks a rostellum, there is some resemblance to a cyst. The structure of this zone, which varies in width, is, however, not that of a cyst wall, but rather that of disintegrating protoplasm. A similar layer separating the pellicle from the wood-containing cytoplasm occurs in some individuals of Devescovina, Stephanonympha, and Calonympha, which are probably degenerate. In the intestine of the host, some moribund flagellates are most likely normally present, and the manipulations of smear-making certainly produce degenerative changes in some specimens. Consequently, although several specimens similar to that drawn by Kofoid and Swezy as a cyst of P. multinucleata have been found, these do not seem to the writer to afford convincing evidence for the occurrence of encystment in P. kofoidi.

A striking difference between the two species of Proboscididiella concerns the micro-organisms adherent to the surface of the body. In P. multinucleata the authors state (p. 311) that 'the surface of the body is generally covered with a dense coat of vertically attached bacteria', and their figure shows rather long, rod-like forms. Possibly these are spiral organisms similar to those of certain species of Oxymonas, as these often appear like rods in fixed material. On the body of P. kofoidi there are instead short, slightly curved, rod-like micro-organisms. In a few cases these are absent, in others there are a few limited chiefly to the posterior region, while in many cases they are abundant on both the body and rostellum (fig. 19, Pl. 22). When sufficiently destained, the interior of these rods is clear, except for several large chromatic granules. The rods vary in length, and some are in stages of transverse fission. The micro-organism, which is also present in the gut contents,
has not been observed in the living condition, but it is similar
to a form, abundant in K. hubbardi, which moves with
rapidity. The surface of Joenia annectens is generally
covered with similar organisms in about the same numbers as
those on P. kofoidi.

The nucleus is spherical or more frequently broadly ovoidal
with the longer axis parallel to the longitudinal axis of the cell.
Within the delicate membrane the nuclear material is arranged
in a manner similar to that of Oxymonas (figs. 12, 13, Pl. 22).
Most of the space is occupied by granules of chromatin somewhat
unequal in size and arranged in groups or strands. There seldom,
if ever, is a regular distribution of isolated granules on a reticu-
rum. In the posterior region of the nucleus is a clear space in
which is the karyosome surrounded, frequently, by a number
of radial strands. The karyosome is somewhat irregular in
outline; often it is broadly ovoidal with the longer axis trans-
verse to the longer axis of the nucleus. The periphery is often
more deeply stained, like a shell, and in the interior may be
clear spaces. Sometimes there seems to be a central granule
(figs. 34 a, 35, Pl. 24), such as that shown in P. multinucleata,
but it is by no means certain that the structure really exists.
At any rate there is so far no convincing evidence that a cen-
triole exists within the karyosome. Besides the karyosome there
may sometimes, but not often, be one or more similar masses
in the nucleus.

The nucleus measures from 4 to 9, usually 6 to 7, microns in
diameter, thus being of about the same size as that of the type
species. The karyosome, however, is proportionately larger
than in that flagellate. While, according to the text (Kofoid and
Swezy, 1926, p. 304) the diameter of the karyosome in their
species is not greater than one-fifth of the diameter of the
nucleus, and is often smaller; that of this form usually measures
fully a third and ranges from a quarter to a half of the nuclear
diameter. On a set of smears prepared from T–234 the nuclei
were smaller, 4 to 5 microns, and the karyosome diameter
0·2 to 0·25 of this. While less than that in the other race, this
is still greater than that of P. multinucleata.
The fibrillar, or neuromotor, system consists of the same elements described by Kofoid and Swezy, but the arrangement of some of these is different. The numerous fine cytoplasmic fibres (figs. 11, 18, Pl. 22), termed by Kofoid retractor fibres, are not limited to the peripheral cytoplasm, as in P. multinucleata, but extend longitudinally throughout the endoplasm. Apparently they begin in the rostellum, where they constitute some of the rostellar filaments, run past the nucleus, and approach close to the posterior end of the body. Sometimes several of these cytoplasmic fibres are collected into a bundle.

Peripheral to the cytoplasmic fibres are the axostyles (fig. 20, &c., Pl. 23), which usually equal the nuclei in number, though often there are several more. Excepting in small individuals, in which the rostellum is short or absent, the axostyles do not reach the posterior end of the body, and may stop far short of this. Each axostyle is flattened, lies just under or in the ectoplasm, and is often turned outward at the posterior end to approach the pellicle, through which the tip may project. There is often some variation in the proportional length and thickness of axostyles in the same individual, and there may be considerable variation in this respect between those of different individuals (cf. figs. 11, 18, Pl. 22). After bending around the upper side of the nucleus, the axostyle tapers abruptly close beneath one of the blepharoplasts and gives origin to several fibres which continue into the rostellum (figs. 28, 29, Pl. 23). The axostyle seems to be composed of fibres, for some are split into several or divided completely up to the region of the blepharoplasts (figs. 22, 23, Pl. 23). In some cases the posterior end has a structure like that of the axostyle of Oxymonas, an arrow-shaped enlargement with a ring around the broader portion, and the part adjacent to this may be divided into several fibres (fig. 14, Pl. 22). It seems probable that the posterior portion, just described, has been lost in most instances, leaving only the tapering, more deeply staining portion (cf. p. 374).

It is by no means certain that the axostyle-like structures in Proboscidiella and Oxymonas are of the same nature as the axostyles of Trichomonas and Devescovina. They
rather resemble the 'axostyles' of Pyrsonympha and Dinenympha, and perhaps the 'chromatic basal rod' of Devescovina. Like these, they stain deeply with iron alum haematoxylin, and not with Delafield's stain; like that of Pyrsonympha they may break up into fibres.

In the arrangement of blepharoplasts and flagella P. kofoidi differs from the type species. In the latter, according to the authors, 'the centrosome lies directly on the anterior face of the nuclear membrane. From it there passes anteriorly a short, delicate rhizoplast to the blepharoplast bar, from whose proximal end, constituting the primary blepharoplast, arises the single primary flagellum, while from the distal end, the secondary blepharoplast, emerges the pair of equal, secondary flagella'. The length of the flagella is shown as not more than three times the diameter of the nucleus, which is about six microns.

In P. kofoidi there are, in each mastigont, arising in pairs from the two blepharoplasts, four flagella of a length (about 60 microns) often equal to or exceeding that of the body (fig. 11, Pl. 22; figs. 20, 25, 27, Pl. 23). In this number and relative length of flagella this oxymonad agrees with several species of uninucleate oxymonads which the writer has observed (p. 359). Thus each single mastigont of the multinucleate form agrees in this particular with the uninucleate form, as is to be expected from the probable close evolutionary relationship between these flagellates.

In each mastigont the two blepharoplasts, which are some distance apart, are unequal in size and shape (fig. 27, Pl. 23). The larger primary blepharoplast, which is close to the anterior end of the nucleus and lies over the axostyle at the point where this narrows abruptly (figs. 28, 29, Pl. 23), is elongated and more pointed at the end opposite to that from which the two flagella arise. From this pointed anterior end there extends into the rostellum a fibre, the proximal section of which, when stout and deeply stained as it frequently is, appears as an oblique bar (fig. 27, Pl. 23). Situated more anteriorly and to the left of the primary blepharoplast is the more spherical secondary blepharoplast, from which also a fibre extends toward the rostellum. In
most cases this fibre seems to meet that from the other granule, so that the two blepharoplasts seem to be at the ends of a fork unequal in length and thickness (figs. 27-9, Pl. 23), but since the fibres often run parallel as far as they can be traced, it is probable that they are not actually united. From the posterior end of each blepharoplast, at the outer edges as seen from above, two flagella emerge (figs. 27-9, Pl. 23). From the smaller secondary blepharoplast a filament runs posteriorly; sometimes this seems to meet the membrane of the adjacent nucleus (figs. 30-2, Pl. 23); sometimes it apparently ends freely (fig. 26, Pl. 23).

The fine interconnexions between axostyle, blepharoplasts, and nucleus are much more difficult to determine than are those structures described in the preceding paragraph, so that, although it is possible for the writer to describe them from a few observations, the description may not be entirely accurate. Under the primary blepharoplast the axostyle seems to end in a small enlargement which is connected to the blepharoplast by a very short strand (fig. 26, Pl. 23). Between this blepharoplast and the nucleus there is possibly a rhizoplast (fig. 26, Pl. 23), which seems to end in a granule at the point where it meets the membrane. In contrast to the stout blepharoplast bar described in P. multinucleata is the delicate strand which may sometimes be made out connecting together the two blepharoplasts (fig. 26, Pl. 23).

A brief summary of the above account will indicate how the blepharoplasts, axostyle, and nucleus of each mastigont are connected. The primary blepharoplast is perhaps attached by a rhizoplast to a granule (centrosome?) on the nuclear membrane, to the axostyle by a short strand, and to the secondary blepharoplast by a fine filament. This blepharoplast also gives rise to a stouter filament which passes into the rostellum. From the secondary blepharoplast a similar filament also enters the rostellum, and another passes posteriorly to meet the membrane of the nucleus of the mastigont to the left, or to end freely between this and its own nucleus. To the membrane of that nucleus it may adhere, at some distance from the anterior end, in a manner similar to that in which the rhizoplast bands of
Staurojoenina are attached. Thus, by this and the primary rhizoplast, may the nuclei be suspended in position, if this account is correct.

No parabasal bodies similar to those of many other polymastigote flagellates have been found in P. kofoidi, despite careful search in material treated by methods which clearly demonstrated those structures in Devescovina and Stephanoymphpha on the same slides. In the position which the parabasal body would, if present, occupy a group of granules has sometimes been seen (figs. 25, 31, Pl. 23; fig. 11, Pl. 22). These granules are often in one or two rows, or grouped in a triangular form close to the nucleus near the primary blepharoplast. Similar granules may exist anterior to the nuclei, or scattered about in the anterior part of the body (fig. 25, Pl. 23), but the frequent observation of a group of these in the position mentioned suggests that they constitute a definite structure. Although not quite the same as the parabasal bodies of many other flagellates, this structure is probably of similar nature. No true parabasal body has been seen, to the writer's knowledge, in any oxymonad flagellate.¹

2. Fission and Mitosis.

Multiplication by fission of the body, preceded by separation of the nuclei into two groups, unaccompanied by mitosis, occurs in P. kofoidi as well as in P. multinucleata. The numbers of nuclei in the two groups are generally unequal. Only one instance of equal separation was observed, with six nuclei in each set. Of those with unequal groups, at one extreme was a case in which there were two and three, and at the other extreme one with nineteen and seven nuclei (fig. 33, Pl. 24). In the earlier stages the nuclei have formed two groups, the axostyles are deeper in the body than usual, and the proximal, but not the distal, end of the rostellum is split, or at least the rostellar fibres are separated. Later the rostellum splits to the

¹ Since writing this the author has observed in a species of Oxymonas from Kalotermes clevelandi, fixed in Flemming's fluid without acetic acid, a granular structure exactly comparable to that of P. kofoidi.

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tip, and finally the two processes and two groups of nuclei are at opposite ends of the body, preliminary to final separation. In one case three groups of nuclei were seen in one body, an instance, probably, of multiple fission.

Although a good many instances of mitotic organization have been found, these were limited to a few stages. The earliest changes begin while the nuclei are in their usual position. The chromatin draws away from the membrane, the karyosome moves toward the centre, and the strands of chromatin granules become thicker and more closely packed (fig. 35, Pl. 24). These changes occur synchronously in all nuclei of an individual, and are most frequent on slides where there are other stages of mitotic organization. There are instances of degenerating nuclei in which the chromatin is similarly clumped, but these occur in only one or two nuclei of a group and are different in appearance from the prophase organization stages.

In later stages the rostellum is shorter and the nuclei have migrated from their usual position into the posterior cytoplasm (fig. 34, Pl. 24). Blepharoplasts, axostyles, cytoplasmic fibres and flagella remain in place. It has not been possible to determine whether or not a centrosome, lying upon the membrane, migrates with the nucleus.

In the migrating prophase nuclei (fig. 34, Pl. 24) the chromatin is dispersed and organized into groups and threads of chromatin granules, perhaps following a contraction stage such as that previously described. The karyosomes, which have moved toward the centre of the nuclei, are of the usual size and form, some showing an inner clear region in which, especially under low magnification, there sometimes seems to be a granule. More careful observation, however, renders the existence of this granule doubtful.

Mitosis proceeds in the nuclei free in the cytoplasm, as in Lophomonas, Calonympha, Stephanonympha, and Oxymonas (fig. 37, Pl. 24). Apparently the number of dividing nuclei at least frequently approximates eight. Thus, in six cases of karyokinesis, in which the nuclei had migrated from their usual position, there were 8, 8, 7, 7, 7, and 6 of these. In a
number of others the bodies had been ruptured, the old fibrillar apparatus torn away, leaving in the remaining cytoplasm 10, 7, 7, and 4 nuclei.

The mitotic figures are very different from those of any other flagellates of termites which have been described, except Oxymonas. In the earliest spindle stage observed (fig. 36, Pl. 24), the nuclear membrane, which is more distinct than in the resting stage, is only slightly elongated (about 8 × 7 microns). Within the membrane the most conspicuous structure is the curved centrodesmose, which is about 1.5 microns broad. Where the truncate ends of this touch the membrane, that is indented as if drawn inward. Surrounding the centrodesmose is chromatic material in the form of numerous short, varicose strands or linear groups of granules.

Later the nucleus becomes more elongated and its ends more pointed. No longer is the membrane drawn inward at the ends of the centrodesmose, but rather it is pushed outward. The centrodesmose, which, when sufficiently destained, seems to consist of a stainable shell with a clear core, has become more bowed (figs. 39, 42, Pl. 24), as if its increase in length has been greater than that of the nucleus. The convex margin may appear stouter and stain more deeply, as if there were a coarse, stainable strand there (fig. 42, Pl. 24), but that is not always the case. In some cases there is an indication of a central strand (fig. 40, Pl. 24), but this may be an illusion due to uneven staining of the shell.

Surrounding the centrodesmose is the spindle, with fibres converging to the poles. While the bulk of the spindle is on the concave side of the centrodesmose, it also extends around the convex side (fig. 39, Pl. 24). Apparently there are no definite chromosomes; at least, if there are, these have no regularity of form and are very numerous. In the mass of chromatic material there are some single granules, but more frequently these granules are collected into linear groups (figs. 37a–42, Pl. 24). The chromatin belt may extend continuously from pole to pole, may be more restricted to the equatorial region, or may be separated into two belts as in an anaphase.
In many instances, and possibly in all, there is a mass on the spindle comparable in size to the karyosome (figs. 41, 42, Pl. 24). This mass is often irregular in form, or may be spherical and much like the karyosome of the resting nucleus in appearance, even to the apparent inner granule. In some later spindles this body seems to be constricting in a dumb-bell form.

At about this time there has begun to differentiate what is most likely the new axostyle (figs. 40, 43, Pl. 24). This is a deeply staining strand, tapering to a point at each end and in length about half that of the nucleus. One pointed end is close to the end of the centrodesmose, from which it is separated by the nuclear membrane and a small space in the cytoplasm. No granule nor rhizoplast has been detected at the end of this structure, even in material prepared in such a manner as to demonstrate clearly the blepharoplasts.

A flagellate without a rostellum (fig. 14, Pl. 22), with nuclei and axostyles different in structure from those of most other specimens, may be interpreted as in a stage following mitotic division. The axostyles differ from the usual condition in each having a posterior prolongation consisting of several filaments which finally collect into an arrow-shaped enlargement. Besides the karyosome, many of the nuclei contain one or two other masses similar in size, form, and stainability. It is possible that the posterior prolongation of the axostyle is later lost, and the nucleus takes on the more typical resting appearance. In the cytoplasm of this flagellate are several structures which seem to be degenerating nuclei, as if all the products of mitosis had not survived.

While this series of stages is too incomplete for the solution of several problems of fundamental importance, it makes possible an incomplete interpretation of the type of mitosis. In P. kofoidi nuclear division proceeds in the same general manner as in Oxymonas, in which, however, there are generally more definite chromatin strands. Although no direct evidence as to the origin of the centrodesmose has been obtained, it is probable that this develops from the karyosome, as in Euglenoidina and, according to Janicki, in O. granulosa.
The origin of the karyosome-like body seen on the spindle is obscure. At the time of mitosis the blepharoplasts, flagella, axostyles, and fibres are discarded, and probably new organelles are differentiated.

The existence of an extranuclear division centre in the oxy-monad flagellates, which is to be expected, awaits conclusive demonstration. None has been recorded in Oxymonas nor in Proboscidiella, excepting that Kofoid and Swezy found a granule which they refer to as a centrosome on the nuclear membrane of P. multinucleata and two such granules on the nucleus of O. projector. They were unable, however, to follow the fate of these granules during nuclear division. It has not been possible to detect any centrosomes nor paradesmose in mitotic figures of P. kofoidi, but the material has been limited. Mr. C. C. Zeliff has obtained evidence of the existence of centrosomes and a delicate paradesmose in a uninucleate oxymonad from Rugitermes kirbyi.

8. Racial Differences.

Most of the observations recorded in this paper were made on P. kofoidi from termites of colony T-239, but upon comparison with those from T-234 several differences, most of which have already been mentioned, were detected. On slides prepared in the Canal Zone from the latter colony, the flagellates were smaller, the organelles of attachment longer, the average number of nuclei was less, the nuclei were smaller, the spherical cytoplasmic inclusions were different in number and size, and the body-surface was free of the micro-organisms so characteristic of the others (fig. 16, Pl. 22). While in the flagellates from T-239 the average size was 66 × 46 microns, and forms exceeding 100 microns in length of the body proper were not uncommon, in those from the other colony the average was only 50 × 38 microns, and no individuals of exceptionally large size were observed. Long rostella were more common than in the others, and the average length of twenty of these was 50 per cent. greater. In one case the rostellum was nearly five times the length of the body (220 and 45 microns). In a hundred indivi-
duals the number of nuclei ranged from 2 to 11, averaging 5.97
and with 6 as the median number. Besides being less numerous,
the nuclei were smaller in size, 4 x 5 microns, and the karyosomes
measured only 0.2 to 0.25 of this. The cytoplasm of these
flagellates was, as already mentioned, crowded with large
spherules (p. 364), while in the Proboscidiella examined from
termites of colony T-239 these were smaller and less numerous,
although under normal conditions they may have been the
same. The presence of micro-organisms on flagellates from the
termites brought to New Haven was a constant characteristic,
but these were absent from the other material.

It is, of course, possible that transportation and filter-paper
feeding produced changes in the intestinal flagellates, but it
seems unlikely that those factors would modify any of the
characteristics referred to except the spherules in the cytoplasm.
In comparison with what may occur in other flagellates of
termites treated in a similar manner, it is probable that
the unusual conditions would, if anything, decrease the
size and stimulate division, besides altering the cytoplasmic
contents.

These differences in the flagellates from the two host colonies
may represent racial peculiarities which have developed during
a long period of isolation, or may be within the normal range
of variation. At any rate, this demonstration of the differences
which may occur shows the need of caution in the classification
of similar flagellates, for, if the hosts had been of two species,
specific separation of the two forms of Proboscidiella would
have seemed justifiable. As it is, it seems best to regard the
smaller flagellate as a variety of the species kofoidi, of which
the type is the form from colony T-239.

4. Systematic Position of Species.

The differences between the flagellar apparatus of those
species of uninucleate oxymonads mentioned in the first part of
this paper, and those species of Oxymonas described by
Kofoid and Swezy (1926), lead to some confusion as to the
characters of the group. The former agree in number and
relative length of flagella with each mastigont in *P. kofoidi*, while the latter have twice the number possessed by each neuro-motor unit of *P. multinucleata*. A constant difference in the number of flagella is justification for the separation of genera in many flagellates. No doubt this should also be the case with the oxymonads, unless further study shows that there is greater uniformity than present descriptions seem to indicate. Although the writer was inclined at first to assign the Central American species of multinucleate oxymonad to a new genus, further consideration of the close resemblance in most respects between it and the described species of *Proboscidiella* made it seem more likely that it should rather be placed in that genus. If that is the correct procedure, it is at least necessary to modify the characters of the genus as regards number of flagella to permit the inclusion of this species with four flagella in each mastigont.

5. Diagnosis: *Proboscidiella kofoidi* sp. nov.

Entozoic flagellates with the characters of the genus, but differing from the generic type in having no blepharoplast bar but two blepharoplasts possibly connected by a delicate filament, and two pair of long flagella in each mastigont. The number of mastigonts varies from two to nineteen or more, averaging eight. The body normally contains numerous characteristic spherules, as well as particles of wood. The flagellates are generally attached to the lining of the gut by an anterior prolongation of the body, but may lack that structure and swim in the lumen by means of the long flagella. The average size is about 66 × 46 microns, and the average length of the rostellum about that of the body. Short, rod-shaped micro-organisms are often attached in large numbers to the surface of the body, by one end.

Host: *Kaloterme*es (*Cryptoterme*) *dudleyi* Banks, 1918.
Colony T-239. Locality: Balboa, Canal Zone, Panama.
Variety in *Kaloterme*es (*Cryptoterme*) *dudleyi*. Colony T-234.
Locality: Ancon, Canal Zone, Panama.
(For characteristics see p. 375.)
V. The Genus Microrhopalodina and Grassi’s Flask-shaped Forms of Calonymphidae.

The account of Microrhopalodina enflata given by Grassi and Foa (1911) is very incomplete and lacks illustrations, but it is probable that they were describing a multinucleate oxymonad. This flagellate, according to them, has a brief period of free existence, and a much longer period of attachment to the intestinal lining by a long ‘peduncle’. In the fixed stage the flagella are lost, growth occurs, a flask-form is assumed, and the nuclei, blepharoplasts, and axostyles multiply repeatedly, forming a group at the base of the ‘neck’. From near the nuclei the axial filaments may continue anteriorly to the attached extremity of the neck, and many may run posteriorly into the body. In this stage solid wood is ingested and there are in the cytoplasm numerous round corpuscles which, though not fat, are possibly some reserve material. When the termite moults, the flagellates become detached, the neck disappears, the characteristic corpuscles and wood are discarded, and flagella develop. This form may then divide into small, uninucleate flagellates, which give origin to new attached flask-forms.

From this description, since we receive no information concerning size, number, or structure of nuclei, number or length of flagella, arrangement of blepharoplasts or size of the body, it is impossible to gain a clear conception of Microrhopalodina. Of those flagellates in termites which are known, Proboscidiella agrees most closely with the description, in that the nuclei are located in both at the base of the ‘neck’, for the most part, rostellar and body-filaments are present, the anterior organ of attachment may be well developed or lost, flagella may develop, especially on free forms, and characteristic corpuscles as well as wood particles may be present in the body. Perhaps a re-study of Microrhopalodina will show that it has the same structure as Proboscidiella, in which case the latter name will become a synonym of the former, which will be the type genus of the family.1

1 Through the kindness of Dr. A. E. Emerson, of the University of Pittsburg, the writer has been able to examine two living nymumps of
The uninucleate, rostellate flagellates figured by Grassi in 1917 were regarded by him as stages in the life-history of Calonymphidae, to which family he also assigns Microrhopalodina. The so-called flask-forms of S. silvestrii var. neotermitis erythraei resemble Oxymonas, while the larger flask-forms attributed to Diplonympha foae, which have more highly developed rostella but only one or sometimes two nuclei, are not unlike O. pediculosa and the form from K. panamae. If any more than morphological evidence is needed to show the error, which Bernstein (1928) has pointed out, in Grassi’s interpretation of these flagellates, this is supplied by the fact that in K. minor and K. hubbardi, which harbour uninucleate oxymonads, no Calonymphidae nor other multinucleate flagellates are present.1

The family Calonymphidae, in which Grassi placed the above-mentioned Protozoa, is defined by him as comprising flagellates with many nuclei, many axial filaments, blepharoplasts, and parabasal bodies. While Proboscidiella would be covered by that definition, except for the lack of definite parabasal bodies, Oxymonas would not, and obviously Oxymonas cannot be separated from Proboscidiella. Because of this fact, together with the marked morphological differences, the oxymonad flagellates should be removed from the family Calonymphidae, in which they have recently been included by Bernstein (1928).

VI. The Family Oxymonadidae.

The oxymonad flagellates, which form a unified group with characteristic structures and peculiar distribution, are set apart in several respects from all other flagellates known at present.

K. flavicollis. These were infected with an abundance of Joenia annectens, Hexamastix termitis, Janickiella grassii, and the so-called Trimitus-forms, but no specimens of Microrhopalodina were found.

1 Grasse (1926, p. 572) states that he has found the uninucleate stages of M. enflata in K. flavicollis, and accepts Grassi’s interpretation of similar flagellates as developmental stages of Stephanonympha.
It is therefore very desirable that a family be established to contain them, in order that they may no longer be confused with quite different forms. For convenience in classification the writer proposes the new family Oxymonadidae.

1. Diagnosis: Oxymonadidae fam. nov.

Entozoic flagellates which have an anterior organelle of attachment, the rostellum, possess a characteristic nucleus, and have a peculiar type of mitosis. The nucleus contains a large karyosome and granular chromatin filling the remaining space. During division, there is a stout centrodesmose, which is apparently developed from the karyosome. There are in each mastigont two blepharoplasts, each of which gives rise to a group of flagella (two or three in all cases except P. multinucleata), an axostyle, probably a parabasal (see p. 371), and cytoplasmic and rostellar filaments. The majority of known species are uninucleate, but there are also multinucleate forms of some of these species and multinucleate species. So far as is known at present these flagellates occur only in termites of the sub-family Kalotermitinae, in which they are widely distributed.

2. List of Genera and Species.

(?) Microrhopalodina Grassi and Foa, 1911.
M. enflata Grassi and Foa, 1911.

Host: Kalotermes (Kalotermes) flavicollis Fabr.
Locality: Italy.
(Inadequately described and not figured.)

Oxymonas (Janicki, 1915) emend. Kofoid and Swezy, 1926.
O. granulosa Janicki, 1915.

Host: Kalotermes (Neotermes) connexus Snyder, 1922.
Locality: Honolulu, Hawaii.

O. projector Kofoid and Swezy, 1926.

Host: Kalotermes (Glyptotermes) perparvus Emerson, 1925.
Locality: Kartabo, British Guiana.
O. pediculosa Kofoid and Swezy, 1926.
Host: Kalotermes (Lobitermes) nigriceps Emerson, 1925.
Locality: Kartabo, British Guiana.

O. gracilis Kofoid and Swezy, 1926.
Host: Kalotermes (Rugitermes) magninotus Emerson, 1925.
Locality: Kartabo, British Guiana.

O. parvula Kirby, 1926.
Host: Kalotermes (Cryptotermes) hermsi Kirby, 1925.
Locality: Fanning Island, Central Pacific Ocean.

Proboscidiella Kofoid and Swezy, 1926.
P. multinucleata Kofoid and Swezy, 1926.
Host: Kalotermes (Planocryptotermes) nocens Light, 1921.
Locality: Manila, Philippine Islands.

P. kofoidi Kirby, 1929.
Host: Kalotermes (Cryptotermes) dudleyi Banks, 1918.
Locality: Balboa, Canal Zone, Panama.


Wenyon (1926) separates the monozoic, diplozoic, and polyzoic flagellates as Protomonadida, Diplomonadida, and Polymastigida. In this scheme the Oxymonadidae have no place, for the family includes both monozoic and polyzoic forms, and there would certainly be no justification for distributing Oxymonas and Proboscidiella into separate orders. For them it is better to retain the order Polymastigida, as does Calkins (1926), which includes the polyzoic Calonymphidae, besides other flagellates. Therefore, although in nuclear structure and mitotic division the Oxymonadidae differ from other Polymastigidae, they may be assigned to that order, near the Dineymphidae.
VII. Appendix: List of Kalotermitinae Examined for Protozoa.

Preparations from the following termites of the sub-family Kalotermitinae are available to the writer for the study of intestinal Protozoa.¹

Kalotermes (Calcaritermes) brevicollis Banks, 1918. Barro Colorado Island, Canal Zone.
Kalotermes (Calc.) emarginicollis Snyder, 1926. Estrella, Costa Rica.
*Kalotermes (Cryptotermes) brevis Walker, 1853. Porto Rico.
Kalotermes (Crypt.) breviarticulatus Snyder, 1926. Taboga Island, Panama.
Kalotermes (Crypt.) dudleyi Banks, 1918. Balboa, Canal Zone.
Kalotermes (Crypt.) hermsi Kirby, 1925. Fanning Island.
Kalotermes (Glypt.) barbouri Snyder, 1924. Barro Colorado Island, Canal Zone.
Kalotermes (Kalotermes) clevelandi Snyder, 1926. Ancon, Canal Zone.
Kalotermes (K.) contracticornis Snyder, 1925. Cartago, Costa Rica.
*Kalotermes (K.) flavicollis Fabricius. Europe.
Kalotermes (K.) immigrans Snyder, 1922. Fanning Island.
*Kalotermes (K.) jouteli Banks, 1920.
Kalotermes (K.) minor Hagen, 1858. California.
Kalotermes (K.) panamae Snyder, 1924. Barro Colorado Island, Canal Zone.
*Kalotermes (K.) schwarzi Banks, 1920.
Kalotermes (K.) tabogae Snyder, 1924. Taboga Island, Panama.
Kalotermes (Lobitermes) longicollis Banks, 1918. Taboga Island, Panama.
Kalotermes (Neotermes) holmgreni Banks, 1918. Taboga Island, Panama.
Kalotermes (Rugitermes) kirbyi Snyder, 1926. Cartago, Costa Rica.

¹ For the material from those species which are starred, I am indebted to Dr. A. E. Emerson, Dr. S. F. Light, Mr. G. F. Hill, and Dr. L. R. Cleveland. In preparation of this list I have been assisted by Dr. T. E. Snyder.
*Porotermes (Porotermes) grandis* Holmgren, 1912. Victoria, Australia.

*Kalotermes (Cryptotermes)* species. Gardner Island, Galapagos.

*Kalotermes (K.) species.* Gardner Island, Galapagos.

*Kalotermes species.* Estrella, Costa Rica.

Oxymonad flagellates have been found in all of these excepting *Porotermes grandis*. In addition, oxymonad flagellates have been found in the following species, as recorded in the literature:

Kalotermes (Glypt.) *perparvus* Emerson, 1925. Kartabo, British Guiana.

Kalotermes (Glypt.) *parvulus* Sjöstedt. Africa, near Gold Coast.

Kalotermes (Neotermes) *erytraeus* Silvestri. Eritrea.

Kalotermes (Neo.) *connexus* Snyder, 1922. Honolulu, Hawaii.

Kalotermes (Lobitermes) *nigriceps* Emerson, 1925. Kartabo, British Guiana.

Kalotermes (Planoecryptotermes) *nocens* Light, 1921. Manila, Philippine Islands.

Kalotermes (Rugitermes) *magninotus* Emerson, 1925. Kartabo, British Guiana.

The following species have been investigated for Protozoa but Oxymonadidae have not been recorded. They are not, however, known to be absent.

'Epicalotermes aethiopicus' Silvestri. Eritrea.

Kalotermes (Crypt.) *havilandi* Sjöstedt. Africa, near Nigeria.

Kalotermes (Glypt.) *iridipennis* Froggatt. Australia.

Porotermes (Porotermes) *adamsoni* Froggatt. Australia.

REFERENCES.


Janicki, C. (1915).—"Untersuchungen an parasitischen Flagellaten."
DESCRIPTION OF PLATES 21-24.

All figures were drawn with a camera lucida at magnifications of 1,440 and 2,740, excepting figs. 10, 16a, 18, and 25. The methods of fixation and staining used for each specimen are indicated in the description of the figure as follows: S., Schaudinn's fluid; F., Flemming's fluid without acetic acid; D., Delafield's haematoxylin; H., Heidenhain's iron haematoxylin.

PLATE 21.

Figs. 1-9.—Uninucleate oxymonad flagellates with four flagella. Drawings were made with the camera lucida from dark-field preparations of living material. All figures, except fig. 7, were drawn to the scale of microns. \times 900.

Figs. 1-2.—From *K. hubbardi*. Oxymonads lacking rostella, with four flagella and attached spirochaetes.

Fig. 3.—From *K. hubbardi*. Spirochaetes removed by feeding host with acid fuchsin; some rod-shaped bacteria adherent to body.

Fig. 4.—From *K. hubbardi*. A small rostellate individual, with four flagella and adherent spirochaetes.

Fig. 5.—From *K. minor*. Large number of attached spirochaetes. Flagella not shown.

Fig. 6.—From *K. minor*. Outline drawing showing flagella.

Fig. 7.—From *K. minor*. Anterior end of a crushed but still living individual, showing two flagella from each blepharoplast, axostyle, and nucleus. \times 1,712.

Fig. 8.—From *K. marginipennis*.

Fig. 9.—From *K. tabogae*. 
PLATE 22.

Figs. 10–19.—Proboscidieilla kofoidi sp. nov.
Magnification as stated. Figs. 10 and 19 drawn to adjacent scales; fig. 16 a to scale of fig. 19; figs. 11, 12, and 17 to scale at top; others to scale at lower left.

Fig. 10.—Section of intestine of Cryptotermes dudleyi. Flagellates attached by rostellum to wall. ×490. S.D.

Fig. 11.—Full length of flagella; body filaments; granules in position of parabasal body and at base of rostellum. ×900. S.H.

Fig. 12.—Resting nucleus a is a median optical section; b a surface view. ×1,712. S.H.

Fig. 13.—Resting nucleus. ×1,712. S.H.

Fig. 14.—Individual without rostellum. Arrow-shaped enlargements at ends of axostyles, before which the axostyles are split into fibres. Several possibly degenerating nuclei in cytoplasm. ×900. F.H.

Fig. 15.—Rostellum absent, axostyles and filaments gathered into bundle. Tubular structure at end of bundle not connected to axostyles. ×900. S.H.

Fig. 16.—Variety from colony T-234. a, Very long rostellum, expanded at tip. ×375. S.D. b, Same organism, showing large spherical corpuscles crowding cytoplasm. ×900. S.D.

Fig. 17.—Spherical corpuscles similar to those of fig. 16 b. Note clear areas within and depressions on one side of some. ×1,712. S.D.

Fig. 18.—Large individual, long rostellum expanded at tip, only basal portion of flagella shown. Spherical corpuscles, fibrillar system, and filter-paper fibres in body. ×375. S.H.

Fig. 19.—Micro-organisms adherent to surface of body. These are present generally, but have been omitted from most figures. ×900. S.H.

PLATE 23.

Figs. 20–32.—Proboscidieilla kofoidi sp. nov.

Figs. 20–3 and 25 were drawn to scale on left. ×900. All others to scale of microns on right. ×1,712.

Fig. 20.—Full length of flagella; characteristic corpuscles in cytoplasm, and some which stain deeply. S.H.

Fig. 21.—Three nuclei; characteristic form of rostellum. The flagella are omitted. S.H.

Figs. 22–3.—Splitting of the axostyles into fibres. Fig. 22 is focused on the lower portion, fig. 23 on the upper of the same specimen. Blepharoplasts and rostellar filaments also shown. F.H.

Fig. 24.—End of a broad rostellum, showing rostellar filaments. S.H.

Fig. 25.—Diagrammatic typical figure, showing rostellum, flagella, axostyles, rostellar filaments, cytoplasmic filaments, corpuscles and in-
gested particles in body, and deeply stained granules in position of para-basal body and elsewhere.

Figs. 26–32.—Detailed diagrams showing arrangement of nuclei, blepharoplasts and associated filaments, and origin of flagella.

Fig. 26.—Rhizoplast, interblepharoplast filament, connexion between axostyle and blepharoplast, and filament from secondary blepharoplast to nucleus. F.H.

Fig. 27.—Group of nuclei and blepharoplasts, showing flagella and filaments from blepharoplast to rostellum, one of which is stout at base. Axostyles omitted. S.D.

Figs. 28–9.—Origin of flagella, axostyles with anterior prolongations, filaments from blepharoplasts into rostellum. F.H.

Fig. 30.—Filament from secondary blepharoplasts to nuclei. F.H.

Fig. 31.—Same, and collection of granules in position of parabasal body. F.H.

Fig. 32.—Filament from secondary blepharoplast to adjacent nucleus. F.H.

PLATE 24.

Figs. 33–43.—Proboscidiella kofoidii sp. nov. Fission and mitosis.

The drawings of entire organisms (figs. 33, 34, 37) were drawn to scale near top. ×800. Those of individual nuclei by scale in lower left. ×1,522.

Fig. 33.—Fission. The nuclei have separated into two groups of 19 and 7, and the rostellum has divided. S.H.

Fig. 34.—Nuclei in early prophase, migrating into posterior region of cytoplasm. S.H.

Fig. 34 a.—Nucleus from fig. 34.

Fig. 35.—Condensed chromatin mass. Probably earlier than fig. 34. Flagellates may be seen in which all the nuclei, in the usual position near the blepharoplasts, are in this condition. S.H.

Fig. 36.—Later prophase nuclei in portion of ruptured body. Note indentations in membrane at ends of centrodesmose. S.H.

Fig. 37.—Later prophase nuclei, migrated from anterior region. The blepharoplasts are in their usual position. S.H.

Fig. 37 a.—Single nucleus from fig. 37.

Fig. 38.—Hollow appearance of centrodesmose; spindle fibres and chromatin belt. S.H.

Fig. 39.—Increased curvature of centrodesmose. S.H.

Fig. 40.—Appearance of new axostyle (?) at one pole. S.H.

Fig. 41.—Chromatic mass on spindle. Aggregations of chromatin granules separating into two groups. S.H.

Fig. 42.—Similar. Hollow appearance of centrodesmose; denser stain on convex side; chromatic mass on spindle; groups of chromatin granules collecting toward poles. S.H.

Fig. 43.—Spindle-formed nuclei; development of new axostyles. S.H.