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Wilhelm FOISSNER

Corticale Morphogenese bei *Colpidium kleini* (*Ciliata, Holotricha*)

Cortical morphogenesis of *Colpidium kleini (Ciliata, Holotricha)*

Die Morphogenese der Ciliaten, insbesondere die ihrer corticalen Strukturen, ist ein viel bearbeitetes Gebiet der mordernen Protozoenforschung. Im Verlauf des letzten halben Jahrhunderts wurden eine Vielzahl von interessanten und wertvollen Beobachtungen gesammelt (Corliss 1961, Doflein 1914, Grell 1968, Hutner 1964, Kahl 1930–1935, Klein 1942). Mit brillant ausgearbeiteten Forschungsmethoden und der Elektronenmikroskopie gelang die Klärung vieler physiologischer und morphologischer Details. Trotzdem sind wichtige Phänomene, wie z.B. die Genese der corticalen Strukturen, insbesondere die der Basalkörper, sowie Erregungsleitung und Formbildung im wesentlichen ungeklärt geblieben. Keine der aufgestellten Theorien gelangte zu allgemeiner Anerkennung.

Mit der von Klein 1926 eingeführten Versilberungstechnik begann ein neuer Abschnitt in der Protozoenforschung. Diese Methode ist zweifellos noch immer eine der wichtigsten modernen Untersuchungsverfahren. Die Klein'sche „trockene" Entquellungs-Versilberungsmethode (Klein 1926, 1942) wurde bald nachher von Chatton et Lwoff 1930 wieder durch Fixierung des Objekts abgeändert. Diese sog. „nasse" Methode und viele andere in neuerer Zeit entwickelte ähnliche Verfahren, (z.B. Corliss 1961, Gillies and Hanson 1968, Gelei 1932, Hashimoto 1966, Wolska 1966) sind zur Darstellung des Silberliniensystems aber viel weniger geeignet als die „trockenen" Methoden, (Foissner 1969 b, c, Klein 1932, 1942, Raabe 1967) da feinere Strukturdetails meist zerstört werden.

Die allgemeine Anwendung dieser nassen Methoden und die dadurch bedingten schlechten Präparationsergebnisse führten dazu, dass viele von Klein 1942 festgestellte Besonderheiten des Silberliniensystems von anderen Forschern nicht gefunden wurden. Die von Klein 1942 postulierte reizleitende und formbildende Funktion des Silberliniensystems wird heute allgemein abgelehnt (s.z.B. Überblick bei Jahn and Bovee 1964, Pitelka and Child 1964, Tartar 1967). Neuerdings konnte Foissner 1969 b, c auf Grund von experimentellen Untersuchungen die reizleitende und formbildende Funktion des Silberliniensystems aber neuerlich zeigen.

Die vorliegende Studie beschreibt die corticale Morphogenese von *Colpidium kleini*, wobei besonders die ersten Teilungsanfänge und die Genese der Basalkörper studiert wurden.

Material und Methoden

Die Untersuchungen wurden ausschliesslich an *Colpidium kleini* Foissner, *C. colpoda* (Ehrb.) und *C. campylum* (Stokes) durchgeführt. Diese Arten wurden aus Pflanzenaufgüssen isoliert und auf Heu-oder Salatblattextrakt gezüchtet (Foissner 1969 a). Als Nahrung diente die normale, in der Kultur vorkommende Bakterienfauna.

Zum Studium der Morphogenese kam die vom Autor entwickelte „trockene" Versilberungsmethode (Foissner 1967) zur Anwendung. Diese Methode ermöglicht es, feinste Strukturdetails des Silberliniensystems darzustellen. Sie ist in vieler Hinsicht noch empfindlicher als die Klein'sche Originalmethode. Ferner wurden die Tiere einer genauen Lebendbeobachtung unterzogen.

Die Terminologie richtet sich nach den von Corliss 1959 und Klein 1942 gegebenen Richtlinien.

Ergebnisse

Das Silberliniensystem von *Colpidium kleini* ausserhalb der Teilung

Anlässlich der Erstbeschreibung dieser neuen Colpidiumart (Foissner 1969 a) wurde ihr normales Silberliniensystem eingehend untersucht. Auch auf die normalen physiologisch-funktionell bedingten Veränderungen (Protrichozysten- und Cytopygenregeneration) wurde eingegangen. Somit genügt hier eine kurze Charakteristik.

Das Silberliniensystem von *C. kleini* ist ein typisches Streifensystem (Taf. I 1). Funktionell kann man zwei Gruppen von Fibrillen unterscheiden: die Basalfibrillen, (Meridiane 1. Ordnung, Taf. I 4 M_1) denen die Basalkörper der Cilien angeschlossen sind und die Protrichozystenfibrillen, (Meridiane 2. Ordnung, Taf. I 4 M_2) die mit den Relationskörnern der Protrichozysten (Protrichozystenkörner) in Verbindung treten. Der Normalzustand ist abwechselnd je ein Meridian 1. Ordnung mit Basalkörpern und ein Meridian 2. Ordnung mit Protrichozystenkörnern (Taf. I 4). Die Protrichozystenfibrillen münden etwa in der Höhe des Oralapparates in die Basalfibrillen ein. Wird ein Tier stärkeren Reizen ausgesetzt, so werden die Protrichozysten ausgeschleudert (Bresslau 1921, Klein 1929, 1942). Zur Regeneration bzw. zum Neuanschluss an das Silberliniensystem, teilt sich die Protrichozystenfibrille in zwei oder drei Fibrillen auf, die miteinander anastomosieren (Taf. I 3, 4). Nach erfolgtem Anschluss der Protrichozysten wird die Aufteilung rückläufig. Der Oralapparat besitzt die typische tetrahymenide Prägung; drei adorale Membranellen und eine undulierende Membran (vgl. Taf. III 14).

Das Silberliniensystem von *Colpidium kleini* während der Teilung

Um der Beschreibung eine gewisse Ordnung zu geben, wurde die Morphogenese willkürlich in 12 Stadien zerlegt. Jedes dieser Stadien wird aber durch bestimmte Vorgänge im Silberliniensystem determiniert.

Stadium I (Taf. I 5, 6)

Die ersten sichtbaren Teilungsanfänge im Cortex zeigen sich dort, wo der Oralapparat des zukünftigen Individuums entsteht. Dies konnten auch ver-

schiedene andere Forscher (z.B. Diller 1966, Frankel 1960, Klein 1929, 1936, Wise 1965) feststellen. Taf. I 5 und 6 zeigen wohl das früheste erfassbare corticale Teilungsstadium von *C. kleini*. Etwa in der Mitte des Tieres, (s. Pfeil auf Taf. I 5) im Richtungsmeridian (Gelei 1935) (Wiederholungsmeridian Klein 1942, stomatogenetic kinety Nanney 1966) zeigt sich eine stärker anfärbbare Zone, in der eine Vermehrung der Fibrillenzahl des Silberliniensystems feststellbar ist. Zwischen diesen Fibrillen findet teilweise Anastomosenbildung statt, sodass verschieden kleine Maschen im Silberliniensystem entstehen (s. Pfeil auf Taf. I 6). Der Meridian 2. Ordnung, welcher rechts neben den Richtungsmeridian verläuft, mündet im zukünftigen Oralgebiet in den Richtungsmeridian ein. Nach einer kurzen Unterbrechung setzt er sich aber wieder postriorwärst fort. In der Zone mit dem vermehrtem Fibrillenwachstum ist keine Mengenzunahme der Basalkörper feststellbar. Auch in den Stosspunkten [1] des neu entstandenen Gitters sind keine Kumulierungen argyrophiler Substanz erkennbar. Es erfolgt somit am Beginn der Morphogenese, nur eine Vermehrung der Fibrillen des Silberliniensystems!

Stadium 2 (Taf. II 7, 8)

Die im Stadium 1 besprochenen Veränderungen entwickelten sich weiter. Nun ist ein deutlich ausgeprägtes Engmaschengitter in der zukünftigen Oralgegend sichtbar (Taf. II 7 Pfeil). Dieses Engmaschengitter beschränkt sich auf den Richtungsmeridian und den rechts davon liegenden Meridian 2. Ordnung. Allerdings werden sie durch das Engmaschengitter manchmal etwas auseinandergedrängt und teilweise unterbrochen. Noch relativ selten sind an einigen Stosspunkten dieses Engmaschengitters Kumulierungen argyrophiler Substanz verschiedener Grösse nachweisbar (Taf. II 8 Pfeil). Es sind dies — wie man später sehen wird — frühe Entwicklungsstadien der neuen Basalkörper von der AZM und UM des posterioren Teilungsproduktes (Tochtertier). Interressant ist, dass sich diese Kumulierungen argyrophiler Substanz nur in den Stosspunkten von Silberlinien befinden, und dass diese in den Stosspunkten von Stadium 1 nicht feststellbar waren.

Stadium 3 (Taf. II 9, 10)

Noch immer sind alle Teilungsveränderungen im Silberliniensystem auf den Richtungsmeridian bzw. auf die Stelle des zukünftigen Oralgebietes beschränkt. Das in Stadium 2 festgestellte Engmaschengitter hat sich beträchtlich weiterentwickelt (Taf. II 9). In nahezu allen Stosspunkten dieses Gitters befinden sich Kumulierungen argyrophiler Substanz, die teilweise schon die Grösse von Basalkörpern erreichen (Taf. II 10). Zweifellos sind dies die Basalkörper der zukünftigen AZM und UM. Diese Basalkörper sind im Engmaschengitter noch vollständig desorientiert („anarchic field").

Stadium 4 (Taf. III 11)

In der vorerst regellosen Anordnung der Basalkörper im Engmaschengitter (vgl. Taf. II 10) beginnt nun die Orientierung zu den drei adoralen Membra-

[1] Als Stosspunkte bezeichnet man nach Klein 1942 primär alle jene Punkte im Silberlinensystem, die sich durch das Zusammenstossen von Silberlinien unter einem beliebigen Winkel bilden. Sekundär können Stosspunkte auch durch die Verteilerlinie zbw. durch Überlagerung, der, die Silberlinie aufbauenden Subfibrillen gebildet werden.

nellen und zur undulierenden Membran. Taf. III 11 zeigt, dass am anterioren Ende des neuen Oralgebietes die Bildung der drei Membranellen schon vollendet ist, während am posterioren Ende die Basalkörper noch regellos im Engmaschengitter liegen (s. Pfeil). Ebenfalls noch ziemlich unregelmässig und locker angeordnet sind die Basalkörper der neuen undulierenden Membran (links im Bild). Über die Lage des Oralapparates orientiert Taf. III 12, obwohl hier die Teilungsvorgänge schon etwas weiter fortgeschritten sind.

Stadium 5 (Taf. III 12)

Der Oralapparat des Tochtertieres ist in seinen Grundzügen vollendet. Deutlich sind die drei Membranellen und die undulierende Membran zu unterscheiden. Nun zeigen sich erstmals Veränderungen an den links des neuen Oralapparates befindlichen Meridianen erster Ordnung. In der Ebene des neuen Oralapparates findet sich vorerst nur eine geringe Vermehrung der Silberlinien (ähnlich der, wie bei der Bildung des neuen Cytostoms, vgl. Stadium 1). Diese Vermehrung zeigt sich gleichzeitig an 15 links des Oralapparates gelegenen Basalfibrillen.

Stadium 6 (Taf. III 13)

Auffallende Veränderungen finden sich an den 15 links des neuen Oralapparates gelegenen Meridianen 1 und 2 Ordnung. Zwischen diesen bildete sich ein ausgeprägtes Engmaschengitter aus. In den Stosspunkten dieses Gitters sind viele argyrophile Körner; vermutlich neugebildete Basalkörper. Die zukünftige Teilungsfurche ist im Silberliniensystem schon erkennbar, nicht aber am Tier selbst! Sie werläuft dort, wo sich die Meridiane 2. Ordnung aufspalten (s. z.B. Pfeil auf Taf. III 13). Interessant ist, dass sich je ein Ast direkt mit der Basalfibrille des posterioren Tieres, der andere, sich mit irgendeiner Fibrille des Engmaschengitters verbindet. Auffallend ist die Verdichtung der Basalkörper in der Höhe des neuen Oralapparates. Die Basalkörper stehen hier viel dichter als zuvor. Offenbar wurden neue gebildet. Der Bereich mit den dicht gelagerten Basalkörpern erstreckt sich nur soweit als die zukünftige adorale Depression des posterioren Individuums reicht.

Stadium 7 (Taf. III 15, 16, 17)

Das in Stadium 6 zwischen den Meridianen erster Ordnung festgestellte Engmaschengitter ist grösstenteils schon zurückgebildet. Reste finden sich nahe an diese herangerückt. In dessen Stosspunkten liegen noch vereinzelt argyrophile Körner (Taf. III 16). Auf Taf. III 15 erkennt man, dass die Veränderungen auf die ersten 15 Meridiane links des Oralapparates beschränkt sind. Als Kriterium dienen die Meridiane 2 Ordnung. Wo sie sich, wie in Stadium 6 erläutert, aufgespalten haben, sind diese Veränderungen nachzuweisen. Die nächsten auf Taf. III 15 noch sichtbaren Meridiane zeigen nun einen ganz anderen Teilungsmodus. Es werden nicht so ausgeprägte Veränderungen wie an den anderen Meridianen ausgebildet. Nur ein ganz kleiner Bereich der Basalfibrillen des zukünftigen posterioren Individuums bildet ein Engmaschengitter aus (Taf. III 15 (Pfeil) und das sehr stark herausvergrösserte Detail auf Taf. III 17). Der Verlauf der Protrichozystenfibrillen wird nicht unterbrochen. Sie dienen als Begrenzung des Engmaschengitters und sind mit diesem innig verbunden.

Stadium 8 (Taf. IV 18)

Beginnende Invagination des neugebildeten Oralapparates. Am lebenden Tier ist nun eine deutliche Grössenzunahme und eine geringe Furchung festzustellen. An allen Silberlinienmeridianen lassen sich Teilungsveränderungen nachweisen. Es ist deutlich erkennbar, dass die Veränderungen an den Meridianen rechts des neuen Oralapparates ungleich geringer sind, als es die an den ersten 15 Meridianen links des Oralapparates waren. Die Verdichtungen der Basalfibrillen rechts des neuen Oralapparates erweisen sich bei starker Vergrösserung wieder als ein Engmaschengitter vgl. Taf. III 17). An den Meridianen links des Oralapparates traten keine Veränderungen ein.

Stadium 9 (Taf. IV 19, 20)

Vollständige Invagination des neuen Oralapparates, der somit seine endgültige Prägung erhalten hat. An Taf. IV 20 ist er leider zerstört. Der Oralapparat von Taf. III 14 stammt von einem Tier im selben Teilungsstadium wie das Tier auf Taf. IV 20. Deutlich ist sowohl am lebenden als auch am versilberten Tier die Furchung erkennbar (Taf. IV 20). Die Teilungsvorgänge im Silberliniensystem sind trotz der erst geringen Furchung schon fast abgeschlossen! Die Meridiane von anterioren und posterioren Individuum sind nur noch durch einfache Silberlinien verbunden (Taf. IV 20 Pfeil). An allen Meridianen lassen sich bereits die Protrichozystenfibrillen des posterioren Individuums erkennen. Sie münden in der Höhe des neugebildeten Oralapparates in die Meridiane 1. Ordnung ein (Taf. IV 20). Auf der dorsalen Seite münden sie allerdings erst nahe des apikalen Poles. Das Silberliniensystem der zukünftigen adoralen Depression (die ersten 15 Meridiane links des neuen Oralapparates) ist vollständig ausgebildet. Man vgl. Taf. IV 19 (ein herausvergrössertes Detail von Taf. IV 20) mit Taf. I 2, die die adorale Depression eines Tieres ausserhalb der Teilung zeigt.

Stadium 10 (Taf. IV 21)

Deutlicher Fortschritt der Furchung. Die Silberlinien der adoralen Depression von der Ventralseite nähern sich durch die Furchung den Silberlinien der Dorsalseite (s. Taf. IV 21 Pfeil). Jedoch ist keine Verknüpfung der beiden erkennbar (vgl. Stadium 11).

Stadium 11 (Taf. IV 22)

Das Tier kurz vor der Trennung. Die Furchung ist fast vollendet. Deutlich ist bereits die Verknüpfung der ventralen und dorsalen Silberlinien kurz oberhalb des Oralapparates des posterioren Individuums sichtbar. Der Verknüpfungsvorgang beginnt immer kurz oberhalb des Oralapparates und setzt sich dann bis zum apikalen Pol fort (Taf. IV 22). Eine fertig ausgebildete Verknüpfung von einem in der Interphase befindlichen Individuum zeigt Taf. I 2.

Stadium 12 (Taf. IV 23)

Die Teilung ist vollendet. Das Tier wurde zufälligerweise direkt in Moment der Trennung entquollen. Die axiale Stellung der zwei Oralapparate ist bereits verschoben. Beide Tiere besitzen das arttypische Silberliniensystem und sind beträchtlich kleiner, als das in der späten Interphase stehende Individuum.

Diskussion

Fibrilläre Zustandsform der Silberlinien

Auf Grund von elektronenmikroskopischen Untersuchungen wird heute allgemein angenommen, dass das Silberliniensystem keine fibrilläre Differenzierung, sondern ein System von Pellikulafaltungen bzw. Pellikulaspalten darstellt (Allen 1967, Bradbury 1965, 1966, Metz, Pitelka and Westfall 1963, Pitelka 1961, Pitelka and Child 1964).

Diese Ansicht, die auch von vielen anderen Forschern anerkannt wird, (z.B. Corliss 1961, Grell 1968, Tartar 1967, Wise 1965) hat, wie Foissner 1969 c zeigen konnte, keine genügend fundierte Grundlage. Statt dessen wird angenommen, dass das Silberliniensystem fibrillär ist, aber als ausserordentlich labile Struktur, bei der zur Elektronenmikroskopie notwendigen Fixierung und Vorbehandlung des Objekts, grösstenteils bis zur Unkenntlichkeit dissoziiert. Die von vielen Elektronenmikroskopikern im Cortex (Allen 1967, Dumont 1961, Nilsson 1967, Metz, Pitelka and Westfall 1963, Pitelka 1961, Pitelka and Child 1964) aufgefundenen „feinen Filamente" bzw. die „dichte Zone" werden als das Silberliniensystem bzw. dessen Reste aufgefasst (Foissner 1969 c). Auch die vorliegenden Untersuchungen führen zu einer fibrillären Auffassung des Silberliniensystems (s.z.B. Genese der Basalkörper). Beweise für eine fibrilläre Zustandsform gab auch Klein 1932, 1934–35, 1942, 1958.

Genese der oralen Basalkörper

Ein oft diskutiertes Problem ist die Genese der Basalkörper bzw. Centriolen. Noch immer ist ungeklärt, ob sie durch Neubildung oder durch Teilung aus den vorhandenen entstehen. Die verschiedenen Ansichten und experimentellen Feststellungen sind teilweise verwirrend und gegensätzlich. Klein 1932, 1942, Chatton et Seguela 1940 nehmen an, dass die neuen Basalkörper ausschliesslich in bzw. von den Silberlinien gebildet werden. Sie können sich nicht teilen. Lwoff 1950: Die Kinetosomen entstehen ausschliesslich durch Teilung aus vorhandenen Kinetosomen. Ehret und de Haller 1963 nehmen auf Grund von elektronenmikroskopischen Untersuchungen an *Paramecium* eine „de novo" Entstehung der Basalkörper an. Sie fanden keine Teilungsstadien. Pitelka and Child 1964: Die Tatsachen über die Kinetosomenduplikation erscheinen paradox. Moderne Forschungen weisen aber darauf hin, dass sie durch abrupte Polymerisation aus fibriosen Strukturen, innerhalb eines bestimmten molekularen Milieus gebildet werden. Kimball 1964: Es gibt keine deutlichen Beweise für eine Selbstduplikation der Kinetosomen; ihre Duplikation bleibt ein Problem. Seaman 1962 (zitiert aus Kimball 1964) berichtet von DNA Identifikation in den Kinetosomen von *Tetrahymena pyriformis* und spricht von ihnen als teilende Gebilde. Faurè-Fremiet 1961 findet keine Beweise für eine Teilung oder „Knospung" der Kinetosomen. Frankel 1960 und Curds 1966 vermuten eine Teilung der Basalkörper, betonen aber, dass dafür kein direkter Beweis vorhanden ist. Jerka-Dziadosz 1967: Nucleuslose Fragmente von *Urostyla* sind unfähig zu neuen Synthesen, insbesondere zur Bildung von neuen Kinetosomen. Foissner 1969 b, c: Durch mechanische Verletzungen

verlorengegangene Basalkörper von *Colpidium kleini* werden nicht ersetzt. Schuster 1963 und Satir 1965 konnten an *Naegleria* elektronenmikroskopisch die „de novo" Entstehung der Basalkörper zeigen. Viele Arbeiten (s. Überblick bei Wise 1965) weisen darauf hin, dass neue Basalkörper und Centriolen aus relativ amorphen Körpern entstehen und einen Wachstums- und Differenzierungsprozess durchmachen, bevor sie ihre charakteristische Struktur erhalten. Ganz neue Arbeiten (Gillies and Hanson 1968) ziehen für die Basalkörper von *Paramecium* sowohl eine Neuentstehung (orale Basalkörper) als auch eine Teilung (somatische Basalkörper) in Betracht. Allerdings zeigen ihre Abbildungen die diesbezüglichen Einzelheiten nicht.

Der vorliegende Beitrag zur Morphogenese von *C. kleini* kann erstmals mit Abbildungen die „de novo" Entstehung der oralen Basalkörper beweisen. Wie die Taf. I 4, 6, Taf. II 8, 10 zeigen, wird im Gebiet des zukünftigen Oralapparates zuerst ein Engmaschengitter gebildet (Taf. I 5, 6), indem keine Basalkörper feststellbar sind! Relativ früh, wenn der engmaschige Bereich noch sehr klein ist, finden sich in einigen Stosspunkten dieses Gitters (vgl. S. 131) verschieden grosse Kumulierungen argyrophiler Substanz, (Taf. II 8, Pfeil), die zweifellos frühe Entwicklungsstadien der neuen oralen Basalkörper repräsentieren. In einem etwas späteren Stadium (Taf. II 10), indem das Gitter schon ziemlich gross ist, finden sich in den Stosspunkten dieses Gitters klar ausgeprägt die neuen Basalkörper des zukünftigen Oralapparates. Interessant ist die Tatsache, dass die Basalkörper immer in den Fibrillenstosspunkten des Engmaschengitters entstehen. Dies konnte auch schon Klein 1932 klar zeigen. Diese Beobachtungen lassen sich gut mit der Entstehungstheorie der Basalkörper nach Pitelka and Child 1964 erklären. Es liesse sich vorstellen, dass durch das Aufeinandertreffen zweier Silberlinien während ihres Wachstumsprozesses bei der Morphogenese (vgl. S. 131) dieses bestimmte molekulare Milieu und vor allem auch die Substanz für die neuen Basalkörper (Fibrillen des Silberliniensystems) geschaffen wird. Gut mit dieser These zu vereinbaren ist auch die DNA Identifikation von Seaman 1962 in den Basalkörpern. Dieser Befund kann nämlich nicht nur in Richtung einer Teilung der Basalkörper, sondern allgemein in einer Teilungfähigkeit des Silberliniensystems aufgefasst werden. Dass das Silberliniensystem ein sich selbst teilendes Organell ist, kann nach den Arbeiten von Klein 1932, 1942 kaum bezweifelt werden. Ferner lässt sich eine autoplasmatische Formbildung des Silberliniensystems (Formveränderungen des Silberliniensystems ohne sichtbare Nucleusaktivität) nachweisen (Klein 1942, Foissner 1969 b, c). Somit ist es durchaus wahrscheinlich, dass im Silberliniensystem Spuren von DNA mit empfindlichen biochemischen Methoden nachzuweisen wären. Besonders in den Basalkörpern müsste die DNA dann vermehrt auftreten, da sie ja aus den Material der Silberlinien gebildet werden und somit eine örtlich konzentrierte — biochemisch erfassbare — Ansammlung von DNA bzw. Substanz der Silberlinien darstellen.

Genese der somatischen Basalkörper

Bei den Holotrichen Ciliaten ist die Genese der somatischen Basalkörper ungleich schwerer zu verfolgen als bei vielen Hypotrichen (z.B. *Euplotes*). Denn bei diesen wird durch die ausserordentliche Vielzahl der Basalkörper, vor allen aber dadurch, dass sie sehr eng beieinanderstehen, die Beobachtungs

möglichkeit sehr erschwert. Die Genese der somatischen Basalkörper ist mit der Versilberungstechnik oft nicht eindeutig zu erfassen, da offensichtlich nur geringfügige Veränderungen im Silberliniensystem auftreten. Somit ist auch der Zeitpunkt ihrer Genese schwer feststellbar. Frankel 1960, Evans and Corliss 1964 konnten aber ziemlich sicher nachweisen, dass der Hauptteil der somatischen Basalkörper vor dem Beginn der Stomatogenese gebildet wird; insbesondere am Ende der Cytokinese. Dieser Befund ist sehr wahrscheinlich. Es ist klar, dass kurz nach der Teilung beide Tiere bedeutend kleiner als normal sind (vgl. Taf. IV mit 23). Während des folgenden Wachstumsprozesses müssen auch neue Kinetiden gebildet werden. Die vorliegenden Untersuchungen sprechen ebenfalls für eine Neubildung der Basalkörper am Ende der Cytokinese. Nur bei der Genese der adoralen Depression dürfte eine Basalkörperneubildung während der Teilung stattfinden. Hier bemerkt man mit Beginn der Furchung eine starke Vermehrung der Basalkörper (Taf. III 13, 15, 16). Die Basalkörper stehen dort nur während der Teilung so dicht aneinander (vgl. Taf. I 3, 4, die den normalen Abstand der Basalkörper zueinander zeigen).

Es wird angenommen, dass die somatischen Basalkörper, ähnlich wie die oralen, durch Neubildung in den Stosspunkten der Meridiane 1. Ordnung entstehen. Diese Stosspunkte sind nicht so offensichtlich erkennbar wie bei der Stomatogenese. Sie befinden sich wahrscheinlich in den Silberlinien selbst. Da diese sicher subfibrillär aufgebaut sind, (Foissner 1969 c) könnten durch Überkreuzung einzelner Bündel von Subfibrillen leicht Stosspunkte entstehen. Diese Stosspunkte sind nicht so offensichtlich erkennbar wie bei Klein 1942.

Stomatogenese

Die Stomatogenese vollzieht sich im wesentlichen so wie bei *Tetrahymena pyriformis*. Am Beginn sind die Basalkörper des zukünftigen Oralapparates völlig regellos angeordnet („anarchic field" Taf. II 10). Dies steht im Einklang mit den Feststellungen anderer Autoren bei *T. pyriformis* (z.B. Holz 1960, Williams and Scherbaum 1959.) Frankel 1960 zeigte allerdings klar, dass die Basalkörper des neuen Oralapparates von *Glaucoma chattoni* bereits am Beginn der Stomatogenese eine geordnete Formation aufweisen. Es finden sich also bei so nah verwandten Gattungen wie *Colpidium-Glaucoma* Unterschiede in der Stomatogenese! Die Formierung der im Engmaschengitter vorerst regellos angeordneten Basalkörper ist offensichtlich ein genau geordneter Prozess (Taf. I 6, II 8, 10 III 11). Die adoralen Membranellen werden etwas früher als die undulierende Membran gebildet (Taf. III 11). Alle Basalkörper bleiben während dieser Vorgänge immer mit den Silberlinien des Engmaschengitters verbunden!

Die bisher rätzelhaft gebliebene Umordnung bzw. Organisation der Basalkörper im „anarchic field" zu den Basalkörpern der Membranellen, lässt sich leichter verstehen, wenn das Silberliniensystem als formbildender Faktor in Betracht gezogen wird. Da die Basalkörper während der Stomatogenese immer mit den Silberlinien in Relation sind, muss irgendein Zusammenhang zwischen diesen beiden Organellen bestehen. Es ist sehr wahrscheinlich, dass die Basalkörper entweder im Engmaschengitter wandern und sich so zu Membranellen zusammenschliessen, (aktive Bewegung der Basalkörper) oder,

dass sich das Silberliniensystem selbst verändert, um die Basalkörper in die entsprechende Position zu bringen. In diesen Prozess haben wir noch keinen Einblick.

Genese des „Tochter"-Silberliniensystems

Das Silberliniensystem des Tochtertieres (opisthe) entsteht durch Teilung aus dem Silberliniensystem des Elterntieres (proter). Dabei werden alle ektoplasmatischen Differenzierungen verdoppelt. Nach vollzogener Teilung bekommen die Silberliniensysteme der beiden Tiere durch Wachstum wieder ihre artspezifische Grösse. Während der Teilung ist nur ein geringes Längenwachstum der Silberlinien zu konstatieren. Gegensätzlich sind die Verhältnisse bei der Stomatogenese. Hier findet ausschliesslich ein Wachstum der Silberlinien statt (s. Taf. I, II 6, 8). Die Trennung der Silberliniensysteme von „proter" und „opisthe" erfolgt nach Aktivierung eines Engmachengitters (Taf. III 17). Es bildet sich dann beim anterioren Teilungssprössling eine neue distale Polspitze, beim posterioren die apikale Polspitze (Taf. IV 22).

Wo wird das Material für die neuen bzw. wachsenden Silberlinien gebildet? Diese Frage ist momentan nicht zu beantworten. Man kann jedoch vermuten, dass es aus mehr oder weniger unorganisierten Stoffen zuerst zu argyrophiler Substanz umgeformt wird. Diese argyrophile Substanz könnte dann von den vorhandenen Fibrillen während des Wachstumsprozesses zu Silberlinien organisiert werden. Darauf weisen experimentelle Untersuchungen hin, die zeigen konnten, dass neue Silberlinien direkt aus unorganisierter argyrophiler Substanz entstehen können (Foissner 1969 b, c). Zweifellos müsste diese Organisierung zu argyrophiler Substanz bei einem sich teilenden Individuum aber ganz nahe an einer bereits bestehenden Fibrills erfolgen, da nämlich nirgends freie (z.B. aus dem Cytoplasma kommende) argyrophile Substanz nachweisbar ist. Vielleicht wird das Material für die Silberlinien im Cortex synthetisiert.

Silberliniensystem und Formbildung

Einige Beobachtungen der vorliegenden Untersuchungen führen erneut zur Frage, ob zwischen dem Silberliniensystem und der Formbildung der Zelle ein engerer Zusammenhang besteht. Klein 1932, 1942 postulierte das Silberliniensystem als formbildend. Foissner 1969 b, c konnte durch experimentelle Untersuchungen eine formbildende Funktion des Silberliniensystem wahrscheinlich machen. Neuerdings wird aber ein Zusammenhang zwischen Silberliniensystem und Formbildung allgemein abgelehnt. Keine der neueren Arbeiten über die Morphogenese der Ciliaten, zieht das Silberliniensystem als formbildenden Faktor in die Untersuchungen ein. Statt dessen wird eine führende Rolle der Basalkörper und der ihnen angeschlossenen Kinetodesma während der Morphogenese angenommen (Evans and Corliss 1964, Lwoff 1950, Pitelka and Child 1964, Wise 1965). Der Grund zu dieser Annahme ist, dass sich an ihnen bei den verschiedenen morphogenetischen Ereignissen angeblich immer zuerst irgendwelche Varänderungen finden. Zweifellos zeigen sich aber die ersten Teilungsanfänge im Cortex von *C. kleini*, nicht in einer Veränderung der Basalkörper, sondern in Veränderungen des Silberliniensystems (Taf. I 5, 6, II 7, 8). Ähnliches konnten auch verschiedene andere Forscher an verschiedenen Ciliaten demonstrieren (Klein 1929, 1936,

1942, Raabe 1949, Radzikowski 1966). Andere Strukturen der Kinete werden immer erst nach der Entstehung des Basalkörpers gebildet (Pitelka 1946). Da also die Silberlinien bei der Morphogenese zuerst Veränderungen zeigen, hauptsächlich im Sinne einer Umbildung zum Engmaschengitter, ist es wahrscheinlich, dass sie mit der Morphogenese in engeren Zusammenhang stehen, als heute allgemein angenommen wird. Stark gestützt wird diese Auffassung auch durch die Entstehungsweise der Basalkörper (vgl. S. 135). Hier ist die formbildende Potenz des Silberliniensystems klar erkennbar. Interessant ist auch die Beobachtung, dass die zukünftige Furchungszone, lange vor der eigentlichen Furchung, im Silberliniensystem schon sichtbar ist (s. Taf. III 12, 13). Überhaupt ist die Teilung des Silberliniensystems bei Beginn der Furchung schon mehr oder weniger abgeschlossen (s. Taf. III 15). Dies drängt zu der Folgerung, dass das Silberliniensystem vielleicht die Furchung aktiviert. Eine Klarlegung dieses ungemein wichtigen Problems wäre nur durch Experimente, die das Silberliniensystem an der Teilungsfurche oder überhaupt am ganzen Tier eliminieren oder inaktivieren, möglich. Solche Untersuchungen werden durch die aussergewöhlich grosse Dynamik und die autoplasmatische Formbildung des Silberliniensystems ungemein erschwert (Foissner 1969 b, c, Klein 1942). Vielleicht konnten darum die Untersuchungen von Frankel 1964 und Jerka-Dziadosz 1964, 1965, 1967 über den Mechanismus der Furchung keinen wesentlichen Aufschluss geben. Zweifellos sind aber an der Morphogenese, insbesondere am Furchungsprozess, auch andere Faktoren beteiligt. Grosse Beachtung verdient in diesem Zusammenhang die „Musterhypothese" (pattern hypothesis) von Tartar 1961.

Wie man sich die formbildende Funktion des Silberliniensystems im einzelnen vorzustellen hat, ist noch vollständig ungeklärt. Sicherlich ist aber das bei allen morphogenetischen Prozessen aktivierte engmaschige Silberliniensystem sehr wichtig (vgl. auch Klein 1942). Dieses Engmaschengitter beherrscht im Cortex sehr viele Raumpunkte (s.z.B. Taf. II, 8, III 17). Eine formbildende Funktion des Silberliniensystems wird dadurch sehr erleichtert. Da das Streifensystem nur über ein Engmaschengitter gebildet werden kann (s. auch Foissner 1969 b, c) dürfte auch ein phylogenetischer Zusammenhang der beiden Systemtypen untereinander bestehen.

Zusammenfassung

Es wird die corticale Morphogenese von *Colpidium kleini* beschrieben. Die oralen Basalkörper entstehen de novo aus dem Material der Silberlinien und immer in den Stosspunkten derselben. Bei den somatischen Basalkörpern wird derselbe Entstehungsmodus vermutet. Die ersten Teilungsanfänge im Cortex zeigen sich am Richtungsmeridian an der Stelle des zukünftigen Oralapparates. Durch vermehrtes Wachstum der Silberlinien bildet sich zuerst ein Engmaschengitter. Erst dann erscheinen neugebildete Basalkörper. Aus den genannten Beobachtungen, ist auf eine führende Funktion des Silberliniensystems während der Morphogenese des Cortex zu schliessen. Alle Neubildungen im Silberliniensystem haben das Engmashengitter als Grundlage. Eine fibrilläre Zustandsform der Silberlinien wird postuliert. Die Beziehungen zwischen Silberliniensystem und Furchungsprozess sowie die Entstehung der Silberlinien werden diskutiert.

SUMMARY

The cortical morphogenesis of *Colpidium kleini* is described. The oral basal bodies originate de novo from the substance of the silverlines, and always in their junctions. A same mode of generation is presumed for the somatic basal bodies. The first indications of dividing for the cortex, take place at the stomatogenetic kinety at the position of the future oral apparatus. A narrow-meshed grill arises through increased growth of the silverlines. Then appear new basal bodies. A leading function of the silverline system during the morphogenesis is concluded from the described observations. A narrow-meshed grill is the basis of all new formations in the silverline system. A fibrillar organization of the silverlines is postulated. The relation between the furrowing process and the silverline system, as the origin of the silverlines are discussed.

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LEGENDE ZU DEN TAFELN I–IV

1: *C. kleini*, Ventralansicht mit Oralappart und Exkretionsporus (Ex). Deutlich ist die adorale Depression — im Bild links des Oralapparates — erkennbar. Ca. 1000×
2: *C. kleini*, Ansicht des apikalen Poles. Deutlich ist die Verwachsungslinie (Prä-orale Naht) zwischen den ventralen und dorsalen Silberlinien sichtbar. Ca. 6000 ×
3: *C. kleini*, Teilansicht der Ventralseite. Die Basalfibrillen (Meridiane 1. Ordnung) tragen die Basalkörner. Zwischen je zwei Meridianen 1. Ordnung verläuft eine Protrichozystenfibrille (Meridiane 2. Ordnung). Momentan sind den Meridianen 2. Ordnung keine Protrichozysten angeschlossen, sie erscheinen darum ohne Relationskörner. Ca. 5000 ×
4: *C. kleini*, Teilansicht der Ventralseite. Die Meridiane 2. Ordnung (M_2) haben sich teilweise aufgespaltet (vgl. zu Taf. I) und tragen Protrichozystenkörner. Meridiane 1. Ordnung (M_1) mit den in ihnen liegenden Basalkörpern. Ca. 5000 ×
5, 6: *C. kleini*, Ventralansicht. Das früheste im Cortex erfassbare Teilungsstadium. Im Richtungsmeridian zeigt sich etwa in der Mitte ein vermehrtes Wachstum der Silberlinien (Taf. I 5 Pfeil). Es entsteht dadurch ein mehr oder weniger engmaschiges Gitter (Taf. I 6 Pfeil). Ca. 1600 × und Ca. 6000 ×
7, 8: *C. kleini*, Ventralansicht frühes Teilungsstadium. Im zukünftigen Oralgebiet bildete sich ein schön ausgeprägtes Engmaschengitter. In den Stosspunkten dieses Gitters liegen verschieden grosse Kumulierungen argyrophiler Substanz (Taf. II 8, Pfeil). Es handelt sich hier zweifellos um Vorstadien der neuen, oralen Basalkörper. Ca. 1600 ×
9, 10: *C. kleini*, das zukünftige Oralgebiet hat sich beträchtlich vergrössert. Taf. II 10 zeigt ein deutlich ausgeprägtes Engmaschengitter, in dessen Stosspunkten bereits viele neugebildete Basalkörper liegen. Alle Teilungsvorgänge im Cortex sind noch auf den Richtungsmeridian beschränkt. Ca. 1330 × und Ca. 6000 ×
11: *C. kleini*, der neue Oralapparat des posterioren Teilungssprösslings. Die drei adoralen Membranellen sind teilweise schon fertig ausgebildet. Nur im posterioren Bereich sind das Engmaschengitter und die darin liegenden Basalkörper noch sichtbar. Auch die neue undulierende Membran ist unfertig. Ca. 5500 ×
12: *C. kleini*, Ventralansicht, mittleres Teilungsstadium. Der neue Oralapparat des posterioren Teilungssprösslings ist in den Grundzügen gebildet. Nun zeigen sich Veränderungen an den ersten 15 Meridianen 1. Ordnung, links, in der Höhe des neuen Oralapparates. Hier ist ähnlich, wie in Stadium 1 (Taf. I 6) ein vermehrtes Wachstum der Silberlinien zu konstatieren. Ca. 1300 ×
13: *C. kleini*, Ventralseite, Teilungsstadium. Deutlich erkennbar der neue Oralapparat und die Veränderungen in den Meridianen 1 und 2. Ordnung links davon. Zwischen diesen Meridianen bildete sich ein engmaschiges Silberliniensystem, in

dessen Stosspunkten viele neugebildete Basalkörper liegen. Die zukünftige Teilungsfurche ist im Silberliniensystem schon sichtbar (s. Pfeil), obwohl am lebenden Tier noch keine Furchung erkennbar ist. Ca. 5000 ×

14: *C. kleini*, vollständig ausgebildeter neuer Oralapparat. Deutlich sind die Basalkörper der drei adoralen Membranellen (AZM) und der undulierenden Membran (UM) erkennbar. Ca. 2000 ×

15, 16: *C. kleini*, mittleres Teilungsstadium. Es zeigen sich deutliche Veränderungen an den ersten 15 Meridianen 1. Ordnung, links des neuen Oralapparates. Nahe an diese Meridiane herangerückt finden sich noch Reste des in Taf. III 13 festgestellten Engmaschengitters. In den Stosspunkten desselben bemerkt man neugebildete Basalkörper (Taf. III 16). Ferner ist eine deutliche Zunahme der Basalkörperzahl im anterioren Drittel des posterioren Teilungssprösslings zu konstatieren. Ca. 1000 × und Ca. 5800 ×

17: *C. kleini*, herausvergrössertes Detail von Taf. III 15 (s. Pfeil). Teilung der dorsalen Meridiane 1 und 2. Ordnung. Deutlich ist wieder ein zu diesem Zweck aktiviertes Engmaschengitter zu erkennen. Ca. 7000 ×

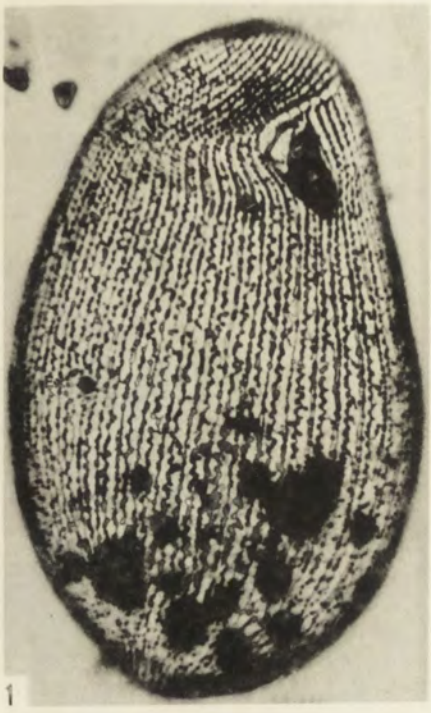
18: *C. kleini*, Ventralansicht, mittleres Teilungsstadium. Es zeigen sich an allen Silberlinienmeridianen in der Höhe des neuen Oralapparates Teilungsveränderungen. Beginnende Furchung und Invagination des neuen Oralapparates. Ca. 1000 ×

19, 20: *C. kleini*, Ventralseite, spätes Teilungsstadium. Die adorale Depression des Tochtertieres ist vollständig ausgebildet (vgl. Taf. IV 19 mit Taf. I 2). Deutlich ist bereits die Trennung der Basalkörperreihen zwischen anterioren und posterioren Teilungssprössling zu erkennen (s. Pfeil). Der neue Oralapparat ist vollständig ausgebildet und invaginiert (vgl. Taf. III 14). Der posteriore Teilungssprössling besitzt schon eigene Protrichozystenfibrillen, die nicht mehr in direktem Kontakt mit denen des anterioren Teilungssprösslings stehen. Deutliche Furchung. Ca. 6000 × und Ca. 1000 ×

21: *C. kleini*, Ventralseite, spätes Teilungsstadium. Die Teilungfurche ist deutlich ausgeprägt. Die Silberliniensysteme von anterioren und posterioren Teilungssprössling sind vollständig ausgebildet. Oberhalb des neugebildeten Oralapparates beginnen die dorsalen und ventralen Silberlinien zusammenzuwachsen (s. Pfeil). Ca. 900 ×

22: *C. kleini*, Ventralseite, Tiere kurz vor der Trennung. Die ventralen und dorsalen Silberlinienmeridane sind oberhalb des neuen Oralapparates zusammengewachsen. Ca. 800 ×

23: *C. kleini*, Ventralseite, Tiere im Moment der Trennung. Die axiale Stellung der beiden Oralapparate ist bereits verschoben. Beide Tiere sind wesentlich kleiner als ein Individuum im der späten Interphase. Ca. 800 ×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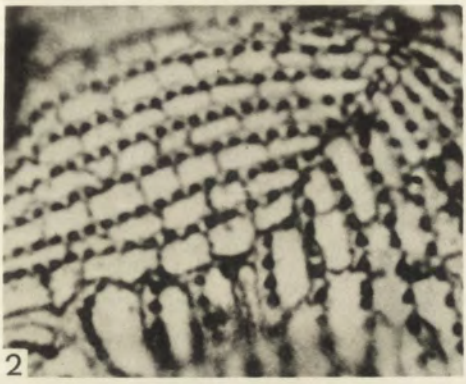
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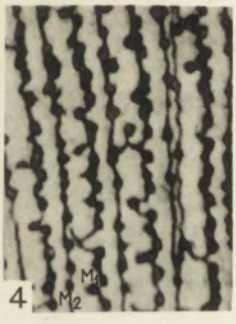

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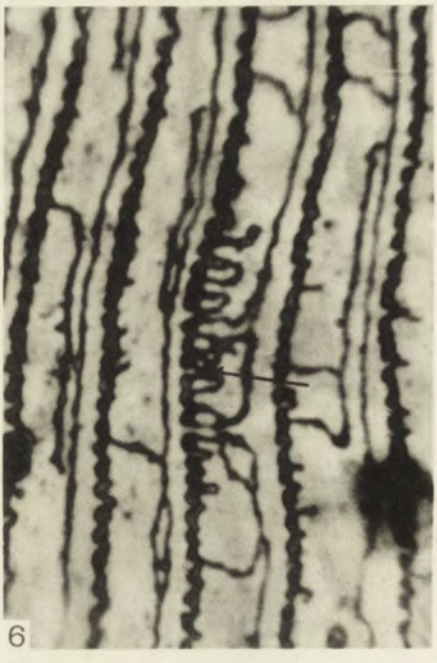
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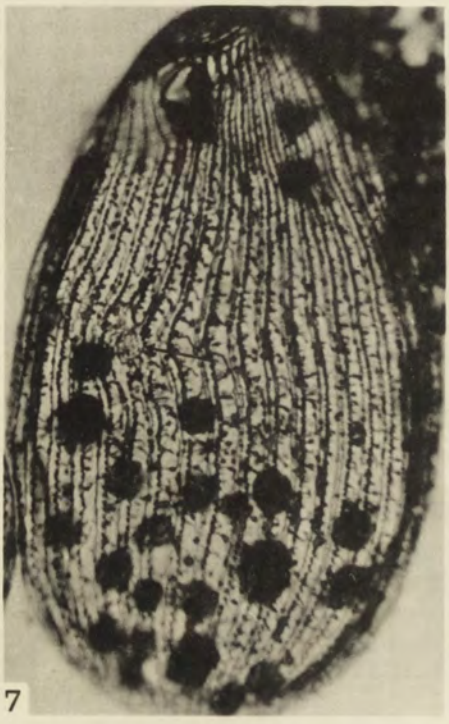
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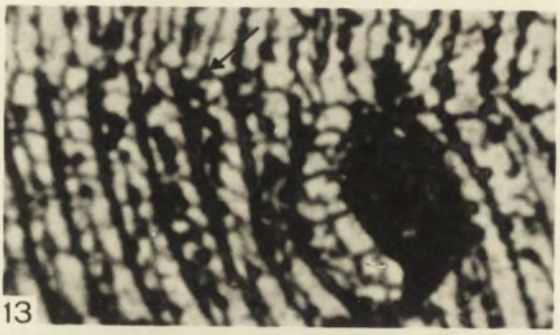
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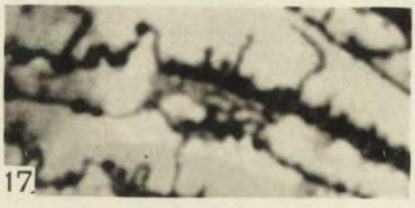
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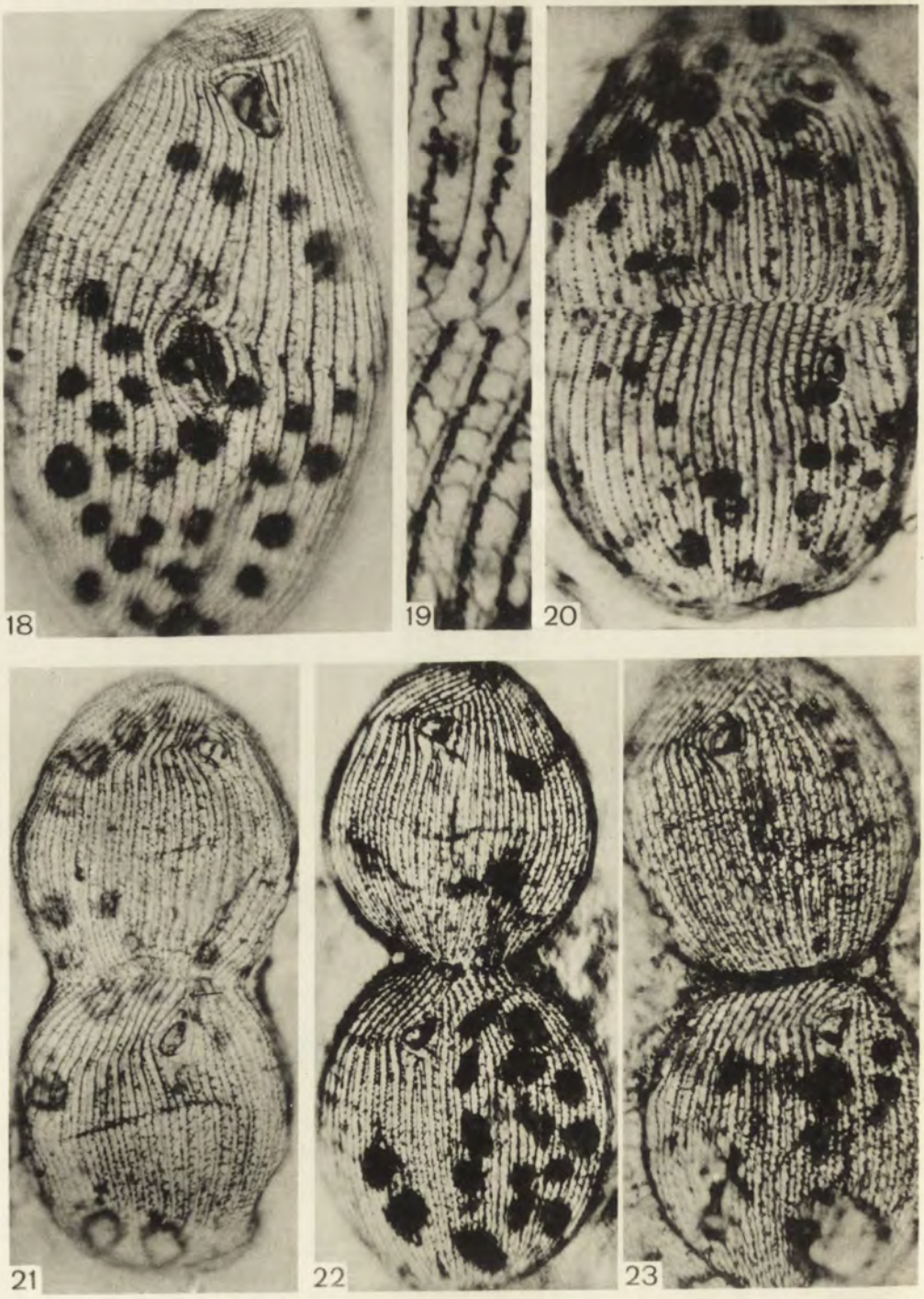

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Maria WOLSKA

Spirocorys indicus Wolska, 1969 a ciliate from the intestine of Indian elephant, its systematic position

Spirocorys indicus Wolska, 1969 orzęsek z jelita słonia indyjskiego jego stanowisko systematyczne

A ciliate was found in Indian elephants from the Zoological Gardens in Warszawa and Łódź.

The samples of elephant feces were fixed in 10 per cent formalin in a capacity exceeding that of the sample. After fixation the material was filtered through the bolting cloth in order to remove a large mass of indigested plant particles. Next, the material was condensed by centrifugation and washed in water. In the material prepared in such way only the shape of ciliates might have been observed if no further procedure had been used. Most of the ciliates were disintegrated. In undamaged specimens the somatic and buccal ciliature and fibers appeared after silver impregnation. In many cases silver precipitated on the nucleus surface also.

The protozoans were impregnated with Bielszowski's silver solution in a thin gelatin layer according to Chatton.

Results

The ciliate is pear-shaped. Narrowed forebody is twisted in form of a cork-screw. The twisting and narrowing of the anterior part may be more or less pronounced (Pl. I 1–3). It is possible that the part of the protozoans described here dilated in the beginning of disintegration process but in every case their forebody was twisted.

Oval macronucleus lies usually in the centre of the enlarged part of the body, sometimes it is shifted to the posterior pole. Round micronucleus lies near to the macronucleus (Pl. I 2).

The body dimensions vary within large ranges. Body length amounts from 68 to 104 μ, body width from 27 to 47 μ. Measurements were made on 18 specimens.

The somatic ciliature is composed of two ciliary zones in the anterior and two zones in the posterior enlarged part of the body. The buccal ciliature is formed of a separate zone.

A shallow groove begins at the top of the ciliate, then it runs spirally backwards surrounding the ciliate body. Gradually it becomes deeper and passes

into a proper buccal concavity, directed backwards, at about one third of the body length. The body side with buccal overture is designed here as a left one. The buccal concavity deeply hollows up cytoplasm reaching at least to the mid-length of the enlarged posterior part of the body. This concavity is horn-shaped, with a top directed to the back and a convexity to the ventral side of the ciliate body.

Both anterior ciliary zones lie along the spiral groove. One of them, the preoral zone, partially covers the forebody. It lies on the ventral side between the anterior margin of the groove and the top of the ciliate. It encroaches conspicuously on the left side and less on the right. The kineties forming the preoral zone are strongly slanted in relation to the longitudinal body axis. They are arranged regularly and closely adjoined to one another (Fig. 1 A, Pl. I 2).

Second anterior ciliary zone, the postoral one, is long. It begins on the left side at the top of the body, dorsally to the former zone. Gradually it becomes broader passing spirally backwards along the posterior margin of the groove. This zone ends on the left side of the body, in the place where the spiral groove passes into a hon-shaped concavity (Fig. 1 A).

On the right side of the body, backwards to the postoral zone lie some kineties with loose kinetosomes (they are named special kineties). Some of them are evidently a prolongation of the postoral kineties, some are separa-

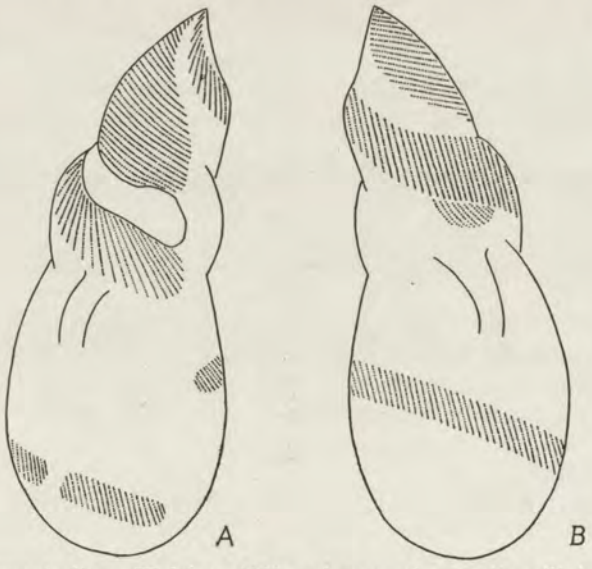

Fig. 1. *Spirocorys indicus* Wolska, 1969, scheme of somatic ciliature arrangement. A — left side, B — right side

ted (Fig. 1 B). These special kineties do not run straight in the direction of postoral kineties but are slightly bent as if they would lay on a protuberance (Pl. II 4). I could not ascertain whether such protuberance really existed.

Posterior somatic zones are in the shape of narrow ribbon formed by kineties oblique to the longitudinal axis of the zone. One of these zones is long it runs spirally over half a distance around the ciliate body. It lies on

the right side of the body (Fig. 1 B) with only small segments going over to the left (Fig. 1 A). The second short zone lies on prolongation of the former one and is situated near the posterior body pole on the left side (Fig. 1 A). From the posterior zones short fibrils run anteriad, paralelly to the body surface (Pl. I 1).

The buccal ciliature lining a part of the right wall of buccal concavity forms an independent zone without any connection with somatic ciliature. The buccal zone begins at the anterior margin of the groove, in the place where it passes into the horn-shaped buccal concavity. In this place the edge of the groove is somewhat convexed anteriorly.

In the anterior part the kineties of the buccal zone are short, dense and run obliquely. When dividing into the narrowing part of the concavity the kineties elongate and change their direction from oblique to paralell to the buccal concavity axis (Fig. 2). The left and ventral walls of the concavity are

Fig. 2. *Spirocorys indicus* Wolska, 1969, anterior end of the body, scheme of buccal ciliature

strengthened by semicircular fibers. It seems that these fibers are connected with buccal kineties (Pl. II 5). The spiral groove leading to the buccal concavity is also lined with fibers running from one side to another (Pl. II 6).

The buccal apparatus of the new ciliate resembles that of *Blepharocorythidae*. This similarity expresses itself the best when we compare this species with more primitive ones (W o l s k a 1967 b, 1968). In the new species, similarly as in *Raabena bella* and *Pararaabena dentata*, short oblique kineties in the posterior part of infundibulum pass into elongated ones paralell to the longitudinal axis of buccal concavity. The position of semicircular fibers is identical. As in the genera *Raabena* and *Pararaabena* the anterior part of the buccal concavity is strengthened by the fibers, in the new species in the spiral groove, which is the initial part of the buccal concavity, similar fibers occur. Longitudinal arrangement of kinetis in posterior part of the buccal concavity is characteristic of all the species of the genus *Blepharocorys*.

I suppose the somatic zones of the species described being homologous

with those of the representatives of *Blepharocorythidae*. The preoral zone would be homologous with a zone of frontal process and the postoral zone with a zone of ventral lip in *Blepharocorythidae*.

The new species differs from the representatives of *Blepharocorythidae* by its body shape but it may be derived from this family. We must assume that the frontal process of *Blepharocorythidae* bent on the ventral side and simultaneously the whole anterior part became twisted and elongated. In consequence of this process the zone of the ventral lip elongated acquiring the shape that occurs in the new species. The part, which had been formerly the anterior part of the buccal concavity in *Blepharocorythidae*, became the spiral groove. The frontal zone of *Blepharocorythidae* displaced, as a result of twisting, on the ventral side in front of the spiral groove.

The relationships of this new ciliate to the family *Blepharocorythidae* is underlined by occurrence of special kineties lying posteriorly to the postoral zone. Such special kineties occur always in *Blepharocorythidae* (Wolska 1966, 1967 a, 1967 b, 1968).

Taking into account the general ressemblance in the ciliature, mainly the ressemblance in buccal apparatus, I regard the new species as closely related to the family *Blepharocorythidae*. It ought to be included provisionally in this family. As this species differs distinctly (by the body shape and degree of development of the ciliary zones) from the representatives of all the genera in *Blepharocorythidae* I find it necessary to suggest creation of a new genus for. it.

Spirocorys Wolska, 1969, diagnosis

Body pear-shaped, with narrowed and twisted anterior end. Non-ciliated spiral groove is followed by buccal concavity in the shape of bent cone opening on the left side in one third of the body length. The somatic ciliature is restricted to four groups of cilia. Two of them lie in the anterior part of the body. One (preoral) zone lies at the anterior edge of the spiral groove, the other one (postoral zone) at its posterior edge. Two remaining groups lie in the posterior part of the body. On the right side of the body, posteriorly to the postoral zone some special kineties occur. In the buccal concavity the ciliature occurs only on the right side. In the wall uncovered with cilia the semicircular fibers occur. Oval macronucleus is situated in the enlarged part of the body, small, round micronucleus lies near to the macronucleus.

The type of the genus: *Spirocorys indicus* Wolska, 1969, a parasite of the intestine of the Indian elephant (found in feces).

Summary

The new species of ciliate, *Spirocorys indicus* Wolska, 1969, found in the feces of the Indian elephant from zoological garden, is described. Its close relationships to the family *Blepharocorythidae* are shown.

STRESZCZENIE

Autorka opisuje nowy gatunek orzęska *Spirocorys indicus* Wolska, 1969, znaleziony w ekskrementach słonia indyjskiego z ogrodu zoologicznego. Wykazany został bliski związek tego orzęska z rodziną *Blepharocorythidae*.

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EXPLANATION OF PLATES I–II

Spirocorys indicus Wolska, 1969

1: General view, focused on the right side. In the posterior part one somatic ciliary zone and fibers are seen, 1000 ×
2: Left side, horn-shaped buccal concavity is seen, 1000 ×
3: Focused on the right side. Preoral and postoral ciliary zones are seen, 1000 ×
4: Focused on the right side. A segment of postoral ciliary zone with special kineties lying posteriorly to it, 2000 ×
5: Isolated kineties and fibers of buccal apparatus, 2000 ×
6: Anterior part of the spiral groove; the fibers lining it are seen, 1000 ×


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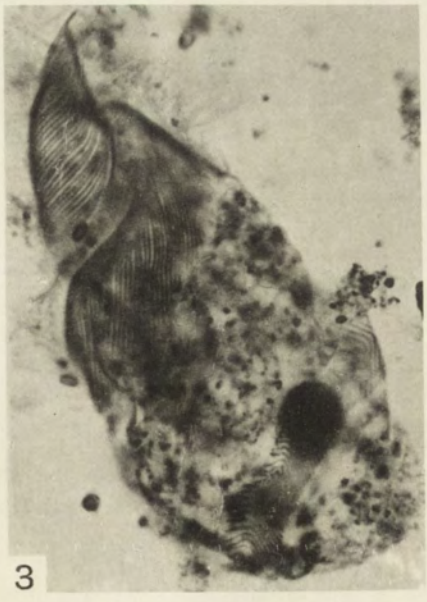
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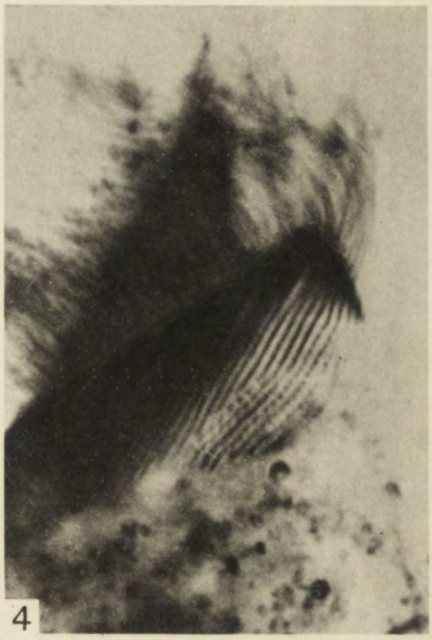
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M. B. JONES and M. A. KHAN

The occurrence of a *Conidophrys* species *(Protozoa, Ciliata)* on members of the *Jaera albifrons* Leach group

L'occurrence d'une espèce de *Conidophrys* (*Protozoa, Ciliata*) sur des membres du groupe *Jaera albifrons* Leach

During an investigation into the ecology and physiology of members of the *Jaera albifrons* Leach group (*Crustacea*: *Isopoda*) collected from Pembrokeshire, a sessile protozoan, which may by tentatively identified as *Conidophrys pilisuctor* Chatton et Lwoff (*Ciliata*: *Conidophryidae*), was seen from time to time attached to antennules, antennae and peraeopods of male and female *Jaera*.

The family *Conidophryidae* (Mohr and LeVeque 1948) contains one genus, *Conidophrys*, and two species, *C. pilisuctor* Chatton et Lwoff and *C. guttipotor* Chatton et Lwoff. Chatton et Lwoff (1934, 1936) first described *C. pilisuctor* as an abundant ectoparasite on *Corophium acherusicum* (Costa) (*Crustacea*: *Amphipoda*) in France, noting also its less abundant occurrence on other amphipods, including *Erichthonius difformis* H. M. Edw. (*Corophiidae*), *Microdeutopus gryllotalpa* Costa (*Aoridae*) Jassa *falcata* Montagu and *J. dentex* Cjerniavski (*Jassidae*), *Gammarus locusta* L. (*Gammaridae*) and *Dexamine spinosa* Montagu (*Dexaminidae*). The same species of *Conidophrys* has been recorded in California from *C. acherusicum* and *Limnoria lignorum* (Rathke) (*Crustacea: Isopoda)* (Mohr and LeVeque 1948) and recently from Scandinavian waters on the isopod *Idotea baltica* (Pallas) and the amphipods *Gammarus locusta* L. and *G. oceanicus* Segerstråle (Fenchel 1965). *C. guttipotor* has been found only in France, where it occurred on the isopod *Sphaeroma serratum* Leach (Chatton et Lwoff 1936).

Apart from an observation of an undescribed *Conidophrys* collected from marine amphipods at Plymouth (Mohr and LeVeque 1948) this is apparently the first record of a *Conidophrys* species from British waters and also its first recorded incidence on members of the *J. albifrons* group. The present investigation includes all the stages described by Chatton et Lwoff 1936 (lacrymoid, spheroid and cucurbitoid stages, and trophont with developing tomites) except the free-swimming young stage. In most details they appear to be similar to the stages of *C. pilisuctor* found on *C. acherusicum* (Chatton et Lwoff 1936). Characters which have not previously been described concern the structure of the thick pellicular covering of the late trophont stages and the mode of attachment of all the stages to the host cuticle. The need to describe these features and the general lack of information about ciliates on

crustaceans in Britain prompted this study of their occurrence on *Jaera*, particularly since the ecological distribution of the host species is now fairly well known (Naylor and Haahtela 1966).

Material and methods

Monthly samples of *Jaera* were taken from Black Tar Beach, a small estuarine shore some distance from the mouth of Milford Haven, South Wales, from October 1968 to April 1969. Isopods were fixed during the collections in either 5% sea-water formalin, or in Bouin's fixative made up in sea-water, and later examined for *Protozoa* in the laboratory using a binocular microscope. Infacted appendages were removed and mounted directly in glycerol, or stained with Heidenhain's haematoxylin using iron alum as a mordant, or impregnated with silver according to the method of Chatton and Lwoff. They were then dehydrated, cleared and mounted in Canada balsam. The stained preparations and also unstained material under phase-contrast (Leitz ortholux) were used to prepare the drawings.

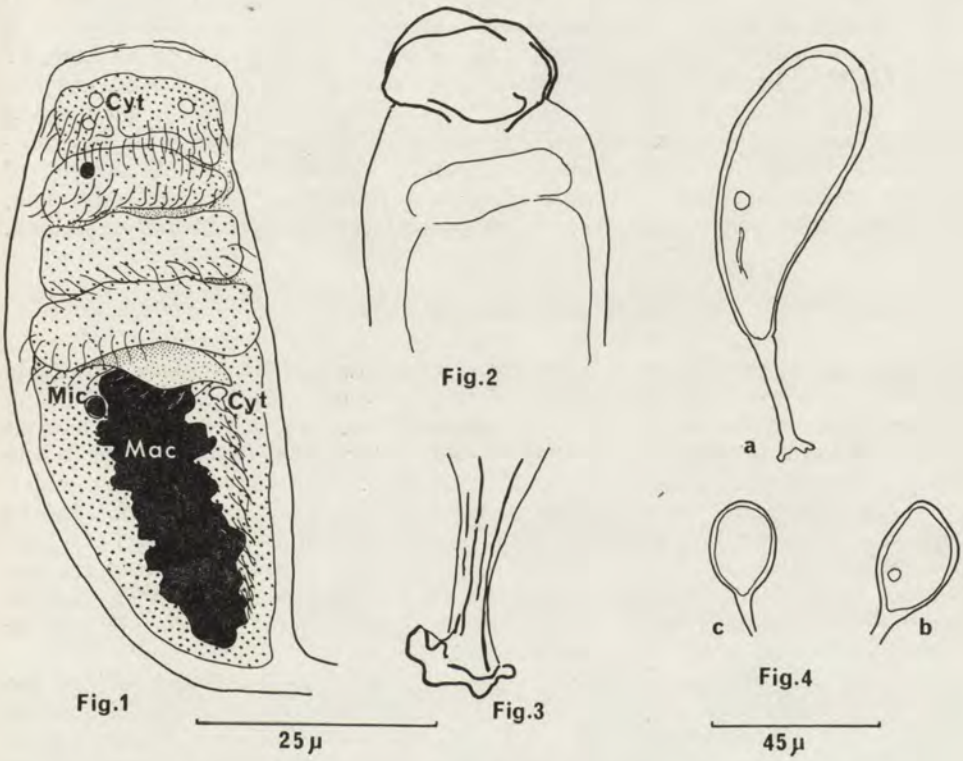
Description

The thick hyaline pellicle, which covers the body and continues posteriorly as a narrow stalk, is present in all the stages found (Figs. 1–4). There appear to be two types of trophont stages. One is vase-shaped, with a permanent funnel-shaped anterior opening, the rims of which are thickened with pellicle (Fig. 2). In the other the pellicle becomes very thin anteriorly and sometimes appears ruptured (Fig. 1). The first type contains only one or two tomites and always has a large space between the tip of the pellicle and the anterior end of the body.

In some specimens the stalk has longitudinal ridges which continue to the base (Fig. 3). It can be hollow or filled with a substance similar to the pellicle. It is almost transparent, not staining with Heidenhain's haematoxylin, and flattened at its distal end to form a base, which has a wavy margin and is attached firmly to the cuticle of the host (Fig. 3).

Each tomite has 1–3 circlets of cilia around its body and a similar ciliary circlet is also present at the anterior end of the trophont stage. The trophont also has two longitudinal rows of cilia which appear to start from the cytopharynx and continue distally to the anterior end of the stalk. The cytoplasm of both the trophont and tomite is basophilic, staining deeply with Heidenhain's haematoxylin, and always contains one or two vacuoles. The macronucleus of the trophont stage is large and irregular, measuring $40\,\mu \times 50\,\mu$, and almost fills the body. The spherical micronucleus has a diameter of $3\,\mu$ and is often found in the distal region of the body (Fig. 1).

The vase-shaped pellicle of the trophont, with a permanent funnel-shaped opening at its anterior end, is one morphological difference from the material described by Chatton and Lwoff. These trophonts, which always have a large space between the tip of the pellicle and the anterior end of the body, are probably late stages where development of tomites has ceased. A very similar structure is seen in the chonotrichid ciliate, *Lobochona prorates* Mohr,



Figs. 1–4. *C. pilisuctor*. 1. A trophont with four developing tomites is shown. Mac — Macronucleus; Mic — Micronucleus; Cyt — Cytopharynx
2. Anterior region of another trophont shows a wide funnel-shaped opening. The pellicle at the margin of the opening is thickened considerably. A gap in the anterior region of the trophont can also be seen
3. The stalk and its base formed by thickened pellicle shows longitudinal ridges. The wavy margin of the base is also clearly seen
4. a.b.c. Three stages of developing trophonts have been seen attached to the antennules in amongst fully developed trophonts. a — cucurbitoid; b — lacrymoid and c — spheroid stage

LeVeque and Matsudo which occurs on *Limnoria tripunctata* Menzies (*Isopoda*) (Mohr et al. 1963) and might easily be confused with *Conidophrys*. The second type of trophont (Fig. 1) has a structure very similar to that of *C. pilisuctor* (Chatton et Lwoff 1936).

The main difference between this material and that of other authors is in the structure of the stalk and the method of attachment to the host. The stalk of the stages found on *Jaera* at Black Tar is often hollow and very similar to that of suctorians. This is clearly seen in the method of attachment by a flattened base which is similar to the base of the stalk of *Acineta tuberosa* Ehrenberg (*Suctoria*) (Guilcher 1951; Kormos et Kormos 1957). The firm attachment of the base of this *Conidophrys* is probably accomplished by an adhesive secretion of the stalk itself as described for many suctorians, peritrichs and chonotrichs (Fauré-Fremiet et al. 1956; Guilcher 1951;

Kormos et Kormos 1957; Mohr, et al. 1963; Precht 1935). Careful examination of stained and unstained material revealed no indication of a "hair" or "bristle" inside the stalk as described by Chatton et Lwoff 1936 for *C. pilisuctor* and confirmed by Fenchel 1965. The total absence of these structures from the stalk of this *Conidophrys*, the different method of attachment to the host and the presence of a trophont stage with a permanent funnel-shaped opening may eventually warrant the establishment of a new species for this material. This must remain a tentative suggestion, however, until suitable numbers of specimens have been found and examined.

Occurrence

Although isopods were collected from all levels and many diverse habitats on the shore, the *Conidophrys* was found only on those animals occurring under stones on the wet parts of the upper shore. This is the typical habitat of *J. albifrons* Leach (Naylor and Haahtela 1966), but the identifiable *Jaera* bearing the protozoan were all males of *J. ischiosetosa* Forsman, which overlaps with *J. albifrons* in that habitat. It is not possible at this time to separate the individual species of the *J. albifrons* group on female characters, identification being solely on the form of the male secondary sexual characters. *J. ischiosetosa* collected during the same period from its typical habitat nearby, i.e. from beneath stones in a small stream crossing the shore (Naylor and Haahtela 1966), were not infected.

The protozoan occurred during October 1968 when it infected 25% of the female isopods (all percentages are expressed for the total numbers of animals collected each month from under stones on the wet parts of the upper shore) and 11% of the males, and in November when it infected 3% of the females and 6% of the male *Jaera*. The absence of the ciliate from subsequent collections may be due to its encystment during the winter months (Chatton et Lwoff 1936). Its presence under stones on the wet parts of the upper shore high up the Milford Haven estuary, confirms the preference of this genus for freshwater to brackish conditions, usually where water movement is minimal (Chatton et Lwoff 1934, 1936; Mohr and LeVeque 1948; Fenchel 1965). It remains to investigate whether the occurrence of the protozoan only on *J. ischiosetosa* away from its typical habitat, reflects merely the sporadic occurrence of the protozoan or whether some other biological explanation must be sought.

We would like to thank Professor E. W. Knight-Jones in whose department the work was carried out and Dr. E. Naylor for helpful discussion. One of us (M.B.J.) is also grateful to N.E.R.C. for financial support.

Summary

A species of *Conidophrys*, which is probably new to science, is recorded for the first time on members of the *J. albifrons* Leach group of species (*Crustacea: Isopoda*), apparently for the first time in British waters. It resembles *Conidophrys pilisuctor* Chatton et Lwoff, except that it is not attached to hairs, but has a pellicular stalk with a terminal attachment disc. Another

difference is that a considerable proportion of trophonts have a funnel-shaped opening in the cyst wall distally. *Conidophrys* seems to be confined to freshwaters and sheltered brackish situations.

RÉSUMÉ

Une espèce de *Conidophrys*, probablement nouvelle à la science, a été enregistrée sur les membres du groupe d'espèces *J. albifrons* Leach (*Crustacea*: *Isopoda*), apparemment pour la première fois, dans des eaux de la Grande Bretagne. Elle ressemble au *Conidophrys pilisuctor* Chatton et Lwoff, cependant elle n'est pas attachée à des cheveux, mais possède une tige pelliculaire à disque d'attachement terminal. Encore une différence se voit en ce qu'une proportion considérable des trophonts, marquent une ouverture en entonnoir à l'extérieur de la paroi du kyste. *Conidophrys* semble se borner à des eaux douces et à des milieux d'eaux saumatres abrités.

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Intestinal flagellates of the common Indian rat *Rattus rattus frugivorous*

Les Flagellès de l'intestin du rat *Rattus rattus frugivorous*

The intestinal flagellates of the Indian rat *Rattus rattus frugivorous* remained unknown until 1963 when T o d d gave an account of some flagellates. The present investigation was undertaken in order to make a complete record of all the intestinal flagellates live in the Indian rat. The following list gives a clear picture of how many species are found in the caecum of this animal:

Caviomonas frugivori sp. n.
Enteromonas ratti sp. n.
Monocercomonoides shortti sp. n.
Monocercomonas hoarei sp. n.
Hexamastix gopali sp. n.
Tritrichomonas frugivori Todd, 1963.
Hexamitus pigmentatus Todd, 1963.
Chilomastix hyderabadensis Todd, 1963.

However, in the present text the consideration is only confined to the new species and they have been described in detail.

Material and methods

For the study of the intestinal flagellates, the rats were thoroughly examined. These animals were supplied by the plague department of Hyderabad City. The animals were brought alive to the laboratory examination. In all the cases they were examined immediately. The intestinal flagellates were generally abundant in the caecum and the intestinal region of the alimentary canal. The movement of the flagellates was studied in fresh condition by the hanging drop preparations.

Eosin, janus green, methylene blue, lugol's solution were always used while making these preparations. Permanent slides were made by both dry and wet methods, which were customarily stained by Giemsa's and haematoxylin stains respectively. In almost all the cases 100 individuals were taken into consideration for measurements from different slides. All the drawings were made with the help of camera lucida at a uniform magnification of × 2000.

Caviomonas frugivori sp. n.

Morphology

The genus *Caviomonas* was erected by Nie 1950 for a flagellate which was observed by him in the caecal content of the guinea-pig *Cavia porcella*. Since that time no other species was added to this genus and this is the second species. In fixed and stained preparations the shape of the body is variable. It is spherical (Fig. 1 G and I), oval (A–C, E, F, H and J) or irregular (D) in

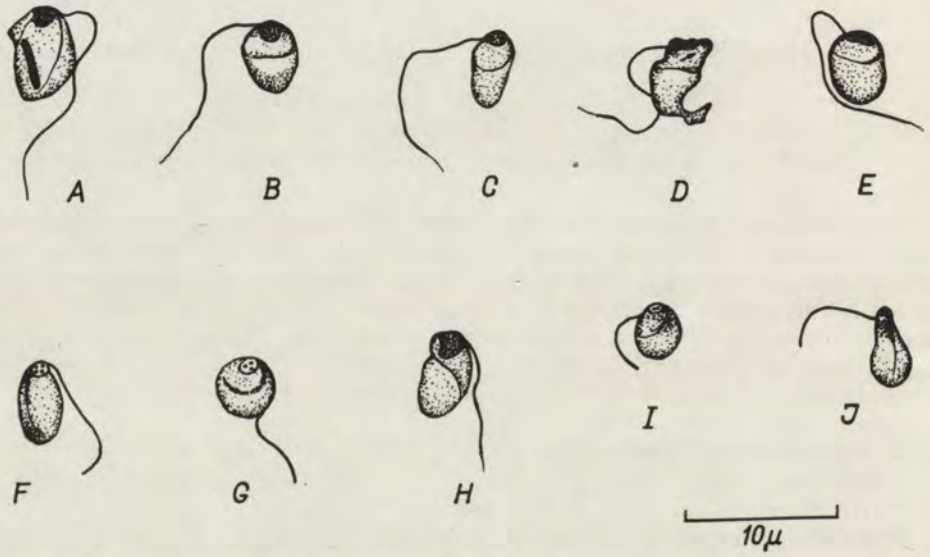

Fig. 1. *Caviomonas frugivori* sp. n. A — Specimen with acronemetic flagellum, peristyle, funis and a large food vacuole; B and C — Showing funis, peristyle and an acronematic flagellum; D — Irregular form showing general structures; E — Showing the blepharoplast and the origin of the mastigont structures; F — Showing three to four compact chromatin granules in the nucleus; G — Showing peristyle which is thick at the origin and thin at the posterior end; H — Showing compact chromatin granules in the nucleus and the peristyle

shape. The length of the body varies from 2.5 to 8.0 μ and the breadth from 2.0 to 5.0 μ. The nucleus is situated at the anterior end of the body which measures from 1.0 to 2.0 μ in length and 1.0 to 3.0 μ in breadth. It is spherical (Figs. 1 A–C and J) oval (G and H) or transversly elongated (D and E) and contains three to four compact chromatin grains. A darkly stained small blepharoplast is situated on one side of the nucleus at the anterior part of the body. A long flagellum originates from this blepharoplast and extends backwards or side-wise but occasionally forwards. It never adheres to the body surface. The flagellum is very long and is three to four times as long as the body. It always terminates in a fine acroneme (Fig. 1 A–D and H). The length of the flagellum ranges from 4.0 to 16.0 μ. A short fine thread like funis arises from the blepharoplast and adheres to the body surface (Fig. 1 A, B and D). A filament like peristyle runs on the opposite side of the funis. It passes along the peripheral surface of the body upto the posterior end (Fig.

1 A, F and J). In some individuals after extending for some distance it curves (Fig. 1 B–E). It is thick at the origin and gradually becomes thinner (Fig. 1 A, E and H). The length of the peristyle is 1.0–4.0 μ. The cytoplasm is granular and vacuolated. It contains food vacuoles within which bacteria and other particles are present.

Discussion

The present parasite differs from the only known species *Caviomonas mobilis* Nie, 1950 in many characters. It is larger than *C. mobilis* and measures 2.5–8.0×2.0–5.0 μ as against 2.2–6.6×2.0–3.3 μ of the latter species. *C. mobilis* has a tail like process at the posterior end which is absent in the present species. In *C. mobilis* the nucleus contains several chromatin granules mostly just beneath the nuclear membrane whereas the present organism the nucleus contains three to four large compact chromatin grains. In Nie's species the nuclear membrane is somewhat drawn out at one point and from there the flagellum arises. The flagellum is two to three times as long as the body and does not terminate in acroneme, while in the new species the flagellum arises from a small blepharoplast which is situated very close to the nucleus. The flagellum is three to four times as long as the body and terminates in a fine acroneme. In *C. mobilis* the peristyle is band like, extends upto the posterior end and projects into a tail-like process, whereas the peristyle of the new species is filament-like and after running along the peripheral surface for some distance it curves inside. The *Caviomonas* of the guinea-pig has a ring like structure in the cytoplasm which is absent in the present species.

In view of the differences cited, it is proposed to name this parasite as *Caviomonas frugivori* sp. n. after the sub-specific name of the host.

Enteromonas ratti sp. n.

Morphology

In stained preparations the parasite is spherical (Fig. 2 A, B, D–H) or oval (J) in shape. It measures from 2.25 to 6.5 μ in length and 2.0 to 6.0 μ in breadth. The nucleus is vesicular and is situated at the anterior part of the body. It is spherical (Fig. 2 B–E) or oval (A, G–J) and the length ranges from 1.0–2.5 μ and the breadth from 0.75–3.0 μ. It contains dense mass of chromatin granules (Fig. 2 E, G, I and J). At the anterior part of the body usually four distinct blepharoplasts are present. They are situated quite away from each other and from each a flagellum arises. Out of four flagella three are directed anteriorly while the fourth one runs posteriorly along the body surface (Fig. 2 A, F and H). The three anterior flagella are unequal in length and are either shorter than the body or equal to the body length. The recurrent flagellum is always longer than the body. Length of the anterior flagella are 2.5–6.0 μ, 2.0–6.0 μ, 2.0–6.0 μ respectively. The length of the trailing flagellum is 3.5–12.0 μ. A filament-like funis arises from the blepharoplast and extends posteriorly upto three fourths of the body length. It is never associated with the recurrent flagellum and the range of length is 2.0–5.5 μ.

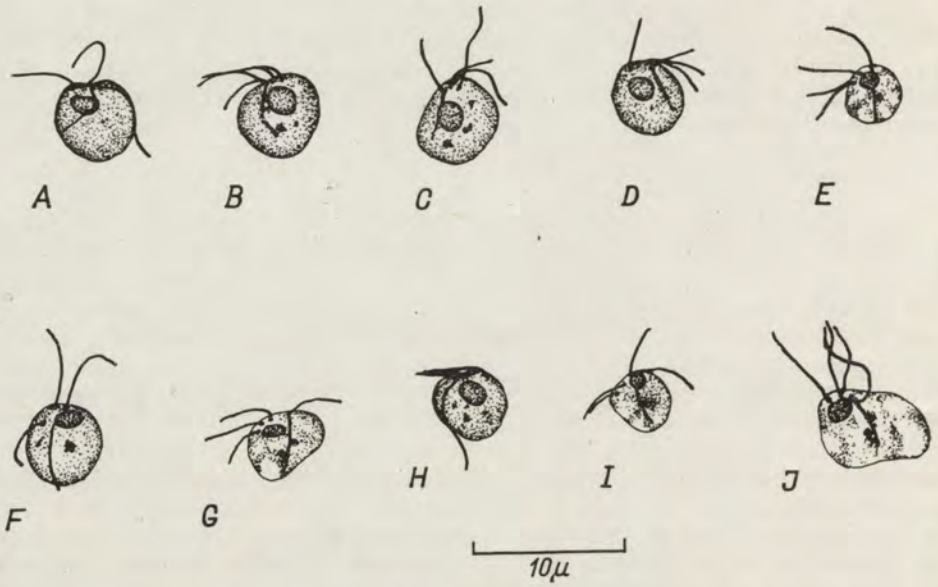

Fig. 2. *Enteromonas ratti* sp. n. A–C — Specimens with three blepharoplasts and four flagella; D — Showing four blepharoplasts, four flagella and a funis; E — Showing chromatin granules in the nucleus, four flagella and a funis; F — Showing the general structures; G, I and J — Showing four blepharoplasts giving rise to four flagella, chromatin granules in the nucleus and a funis; H — Showing a long recurrent flagellum running posteriorly

Discussion

The present *Enteromonas* differs from all other species so far reported in certain characters. *Enteromonas ratti* sp. n. is smaller than *E. hominis* and measures 2.0–6.5×2.0–6.0 μ as against 4.0–10×3.0–6.0 μ of the latter species. The present species has no definite endosome and possesses a dense mass of chromatin granules whereas *E. hominis* possesses a large endosome. The flagellate under discussion has four blepharoplasts and the anterior flagella are unequal unlike Fonseca's species which has a single blepharoplast and the equal anterior flagella.

E. suis (Knowles et Das Gupta, 1929) Dobell, 1935 is 10.0–20.0 μ long and 6.0–14.0 μ broad, and possesses a large nucleus. It has a single blepharoplast and the flagella are very long. But the present species is smaller in size, nucleus very small, blepharoplasts are four in number and the flagella are comparatively short.

E. caviae (Lynch, 1922) Nie, 1950 measures 3.0–5.5×2.3–4.4 μ, the nucleus has an endosome, there is one-two blepharoplasts and the anterior flagella are equal in length, and the funis is closely associated with the trailing flagellum. Whereas the new organism is larger than *E. caviae*, the nucleus does not contain an endosome, the blepharoplasts are four in number, the flagella are unequal in length and the funis is never associated with the recurrent flagellum.

On the basis of the differences mentioned above it is proposed to name this parasite from rat *Rattus rattus frugivorous* as *Enteromonas ratti* sp. n. after the generic name of the host.

Monocercomonoides shortti sp. n.

Morphology

In stained preparations the shape of the body is usually round (Fig. 3 A–D, F, I and J) or pyriform (E, G and H). The length of it ranges from 5.0 to 10.5 μ with an average of 6.96 μ and the breadth ranges from 4.5–9.0 μ with an

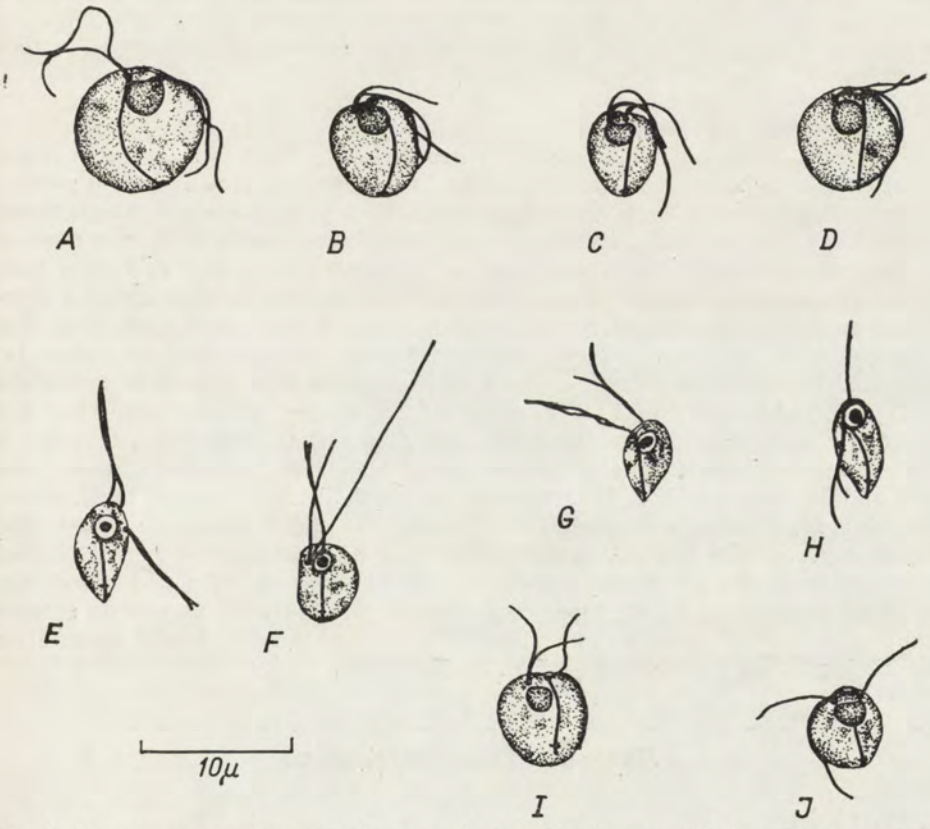

Fig. 3. *Monocercomonoides shortti* sp. n. A–D — Spacimens with two blepharoplasts, thin rhizoplast, origin of the flagella, filamentous axostyle and the axostylar ring; E–H — Showing large endosome in the nucleus; two distinct blepharoplasts and the axostylar ring; I and J — Showing trailing flagellum running posteriorly and the axostyle extending beyond the ring

average of 6.73 μ. The nucleus is situated at the anterior part of the body which is 1.5–3.0 μ long and 5.0–8.5 μ broad. It is generally spherical (Fig. 3 B, D and H) or bean shaped (A, C and J) and contains a large endosome (E and H). At the anterior end of the body between the nucleus and the body wall two large

blepharoplasts are situated from which all the mastigont structures arise. These blepharoplasts are connected by a thin rhizoplast which travels along the margin of the body (Fig. 3 A, C, G, I and J). A pair of four flagella originate from each of the blepharoplasts. Out of four flagella three are directed anteriorly and they are equal in length. The length of the anterior flagella ranges from 3.0–12.0 μ. The fourth flagellum is slightly longer than the three and is always directed backwards. The length of it is 6.0–17.0 μ. All the flagella are uniform in thickness and never terminate in knobs or acronemes. The accessory filament and the pelta are absent. The axostyle is filamentous and originates from the same blepharoplast from which the trailing flagellum arises. It is uniform in thickness but at the posterior region of the axostyle, an axostylar ring is present. In some individuals the axostyle extends beyond the ring (Fig. 3 D and J) but never protrudes outside the body. The length of the axostyle is 5.0–8.5 μ. The cytoplasm is granular and always contains food vacuoles.

Discussion

It is evident that *M. pileata* Kirby et Honigberg, 1949 and *M. sayeedi* Abraham, 1961 come nearest to this organism in dimensions. However, the present parasite differs from them in the presence of a short axostyle which never projects outside the body, the flagella without acronemes and in the absence of an accessory filament. In addition to the above characters, it differs from *M. sayeedi* in the presence of an axostylar ring and in the absence of a cytostome. In the latter character it differs from *M. caprae* Das Gupta, 1935. The absence of an accessory filament distinguishes it from all other species so far reported. In the presence of a short axostyle, the new organism resembles *M. lepusi* Todd, 1963 but it is marked off by having an axostylar ring and a definite endosome in the nucleus. The filamentous axostyle separates it from *M. caviae* (Da Cunha et Muniz, 1921) Nie, 1950, *M. quadrifunilis* Nie, 1950 and *M. wonrichi* Nie, 1950 where it is band-like. In contrast to *M. exilis*, Nie, 1950, *M. digranula* (Crouch 1933) Gabel, 1954 and *M. robustus* Gabel, 1954 the axostyle of the present species never projects outside the body. Further it differs from the latter two species in the absence of pelta and cytostome.

These differences justify the recognition of this parasite as new to science and hence it is proposed to name it as *Monocercomonoides shortti* sp. n. after the distinguished protozoologist Col. H. E. Shortt.

Monocercomonas hoarei sp. n.

Morphology

In stained preparations the shape of the body is spherical (Fig. 4 A, B, D–F), irregular (G and H) or oval (I and J). The length ranges from 5.0–8.5 μ and the breadth from 4.0–7.5 μ. The nucleus is situated at the anterior part of the body. It is been shaped or oval and measures from 1.0–3.5 μ in length and 1.0–5.0 μ in breadth. It contains large and fine chromatin granules (Fig. 4 G and J). At the anterior end of the body there are two blepharoplasts, situated very close to each other. From one of them two anterior flagella originate while from the other the remaining mastigont structures originate. Out of four flagella, three are directed either anteriorly or laterally. They are equal

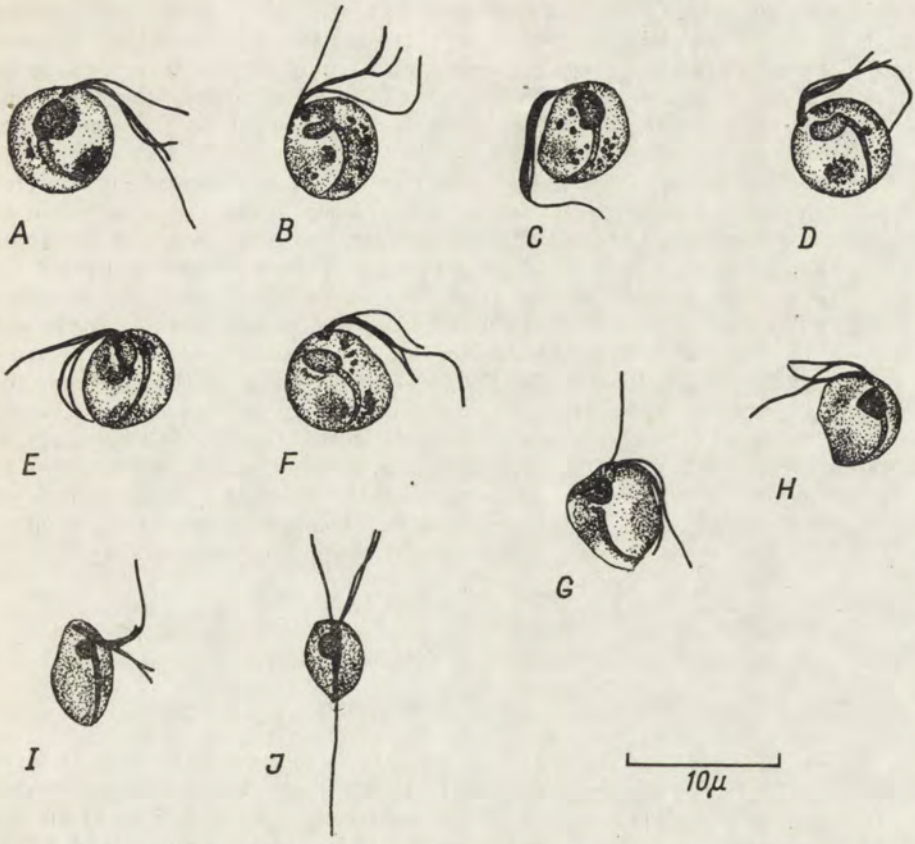

Fig. 4. *Monocercomonas hoarei* sp. n. A–C — Specimens with bean shaped nucleus, curved axostyle, two blepharoplasts, three equal anterior flagella and the long trailing flagellum; D–F — Showing two blepharoplasts and the origin of the flagella; G–I — Showing large and fine chromatin granules in the nucleus; J — Showing the long trailing flagellum running posteriorly

in length and longer than the body. The recurrent flagellum is very long and either passes along with the anterior flagella or proceeds posteriorly. The flagella neither terminate in knobs nor in acronemes. The axostyle originating from the blepharoplast runs beneath the nucleus and extends posteriorly but never projects outside the body. The posterior end of the axostyle usually curves inside the cytoplasm. It is slightly broad at the anterior region and tapers towards the posterior end. The cytoplasm is filled with many granules.

Discussion

This organism shows some marked differences when compared with the forms described earlier and they are as follows: *M. caviae* (Davaine, 1875) Nie, 1950 has only one blepharoplast, the flagella terminate in knobs and the axostyle has an axostylar ring whereas the present species has two blepharoplasts, the flagella never terminate in knobs and the axostyle has no ring. In *M. cuniculi* Tanabe, 1926 the nucleus contains a large endosome. There is

a single blepharoplast, and the cytostome is present while in the new species there is no endosome and cytostome, and there are two blepharoplasts. *M. verrens* Honigberg, 1947 has a large endosome in the nucleus, the anterior flagella terminate in knobs, the trailing flagellum ends in an acroneme, the cytostome and the pelta are present. The present species is lacking all the above mentioned characters. In *M. pistillum* Nie, 1950 there is only one blepharoplast and the flagella terminate in knobs. The posterior end of the axostyle is rounded like a pistle and the siderophilic bodies are present in the cytoplasm. But in the present species there are two blepharoplasts, the flagella never terminate in knobs, the axostyle terminates into a point and the siderophilic bodies are absent. The present parasite differs from *M. minuta* Nie, 1950 in the presence of a larger nucleus, presence of two blepharoplasts, conspicuous axostyle and in the absence of siderophilic bodies in the cytoplasm. It also differs from *M. lori* Abraham, 1962 in the absence of four plaques in the nucleus, the trailing flagellum not terminating in acroneme and the axostyle not projecting beyond the body. Unlike the present species *M. gerbilli* Todd, 1963 has a single blepharoplast and the axostyle is filamentous.

By the above comparison it appears that the present species is new to science and therefore it is designated as *Monocercomonas hoarei* sp. n. after Dr C. A. Hoare, who has made valuable contribution to protozoology.

Hexamastix gopali sp. n.

Morphology

In stained preparations the shape of the body is round (Fig. 5 A, B, D, E, G and H), angular (C) or pyriform (F and I). In all, the anterior end is broader than the posterior end. The length of the body ranges from 6.75 to 14.0 μ the average being 9.58 μ and the breadth from 3.0–12.5 μ with an average of 8.33 μ The nucleus is situated at the anterior end of the body in the vicinity of the capitulum. It is spherical (Fig. 5 D, E, G and I) or elongated (A–C and F) in shape. The length of it is 1.5–5.0 μ and the breadth is 1.5–4.0 μ. There are two large blepharoplasts at the extreme anterior end of the body situated very close to each other. The five anterior flagella originate from one blepharoplast while from the other the trailing flagellum arises. Out of six flagella, five are directed anteriorly or laterally and the sixth flagellum extends posteriorly. All the anterior flagella are equal in length and are equal or shorter than the body length. Sometimes they unite at the base and form a bundle. The trailing flagellum is independent and is equal or shorter than the body. The length of the anterior flagella is 4.0–14.0 μ and the trailing flagellum is 6.0–14.0 μ. The axostyle originates from the blepharoplast and extends upto the posterior end of the body but never projects outside. It has a typical bend in the middle and thus forms a crescent shape. The axostyle has three distinct regions: the capitulum, the trunk and the terminal tip. The capitulum is spoon shaped (Fig. 5 A, C and E), the trunk is uniform in diameter throughout its course and the terminal tip ends in a fine point. The length of it is 4.0–14.0 μ. The cytostome is "V" shaped and is situated on the lateral side of the body very close to the nucleus (Fig. 5 H). The cytoplasm is granular and contains many food particles. The pelta is absent.

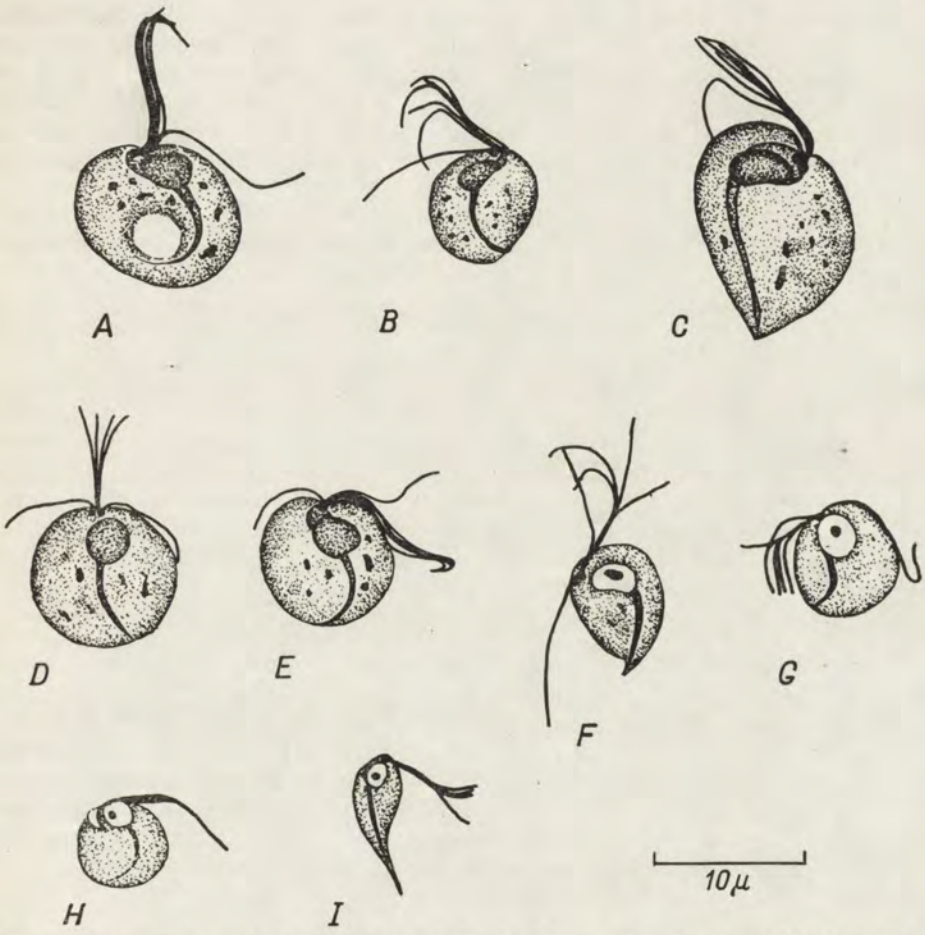

Fig. 5. *Hexamastix gopali* sp. n. A — Spherical form showing two blepharoplasts, a bundle of anterior flagella, an independent trailing flagellum and a curved axostyle; B and C — Showing elongated nucleus, two blepharoplasts, one giving rise to the anterior flagella and the other to the trailing flagellum; D — Spherical form showing two distinct blepharoplasts, short flagella and the axostyle not projecting outside the body; E — Showing the general structures; F — Showing pointed posterior end, elongated nucleus with elongated endosome and two blepharoplasts; G — Showing a small spherical endosome in the nucleus. H — Showing a "V" shaped cytostome; I — Pyriform showing a long pointed posterior end

Discussion

The present species is the largest one described so far. Apart from dimensions the most distinguishing characters of this parasite are — the large nucleus which contains an endosome without any granules around it; two blepharoplasts; anterior flagella and the trailing flagellum equal to or shorter than the body; the axostyle never projects outside the body. In the absence of pelta it differs from all other species.

Apart from these common differences, it differs from some species individually in certain other characters. In *H. muris* Wenrich, 1930 the trailing

flagellum ends in an acroneme, whereas in the present species the trailing flagellum is not acronemetic. The anterior flagella of *H. caviae* Nie, 1950 and *H. robustus* Nie, 1950 possess terminal knobs but in the new species they are absent. *H. cryptonucleata* Crouch, 1933 has a thin hyaline axostyle while in the new organism the axostyle is conspicuous with three distinct regions. A filamentous axostyle is present in *H. scuiri* Todd, 1963. But in the present species the axostyle has a broad capitulum.

From the considerations of dimensions and morphology of the parasite it appears justified in considering the species as new to science. It is therefore named as *Hexamastix gopali* sp. n. after Prof. Gopal Rao, V. Osmania Medical College, Hyderabad.

Acknowledgements

The author wishes to express her sincere gratitude to Prof. S. S. Quadri, Ph. D. (London), Osmania University, under whose supervision the entire work was carried out. She is grateful to Prof. S. N. Singh, D. Sc. (London), F.N.I., Head of the Zoology Department, Osmania University, for the laboratory facilities provided in the department. She is thankful to the Council of Scientific and Industrial Research, New Delhi for the award of a Research Fellowship during the tenure of her research programme.

Summary

A more definite data of all the intestinal flagellates that inhabit the common Indian rat *Rattus rattus frugivorous* is given. However in the present text only the new species are described. According to the present investigation five species — *Caviomonas frugivori* sp. n., *Enteromonas rutti* sp. n., *Monocercomonoides shortti* sp. n., *Monocercomonas hoarei* sp. n., *Hexamastix gopali* sp. n. are new to science. All these species were abundant in the host.

RÉSUMÉ

Des données plus definies concernant le Flagellés inhabitant le rat *Rattus rattus frugivorous* sont citées. Néanmoins dans le texte ci-present seulement les éspèces nouvelles sont décrites. Selon recherches présentes cinq éspèces, dont: *Caviomonas frugivori* sp. n., *Enteromonas ratti* sp. n. *Monocercomonoides shortii* sp. n., *Monocercomonas hoarei* sp. n., *Hexamastix gopali* sp. n., sont nouveaux pour la science. Toutes ces éspèces étaient abondantes dans l'hote.

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Studies on *Myxosporidia (Protozoa, Sporozoa)* from the food fishes of Bengal. I. Three new species from *Ophicephalus punctatus* Bloch

Studien über Myxosporidien (*Protozoa, Sporozoa*) der essbaren Fische von Bengal. I. Drei neue Arten von *Ophicephalus punctatus* Bloch

Several species of myxosporidians (*Henneguya ophicephali* Chakravarty, 1939; *Myxobolus ophicephali, M. aligarhensis, Unicauda basiri* and *Henneguya zahoori* Bhatt et Siddiqui, 1964) have so far been described from the fresh water Indian teleost *Ophicephalus punctatus*. Our present communication records three new species of *Myxosporidia* from the same host hitherto undescribed. Type specimen have been deposited in the Protozoology Laboratory of Calcutta University, Calcutta, India.

Materials and methods

The fishes were obtained from the local market and also from tanks in and around Calcutta. These were kept in the aquaria of the laboratory and examined for myxosporidian parasites.

Macroscopic examinations of the fishes were undertaken for the presence of cysts. Cysts were removed carefully from the host with the help of fine needle and forceps. Microscopical examinations of the internal organs such as gall — and urinary bladders, liver, spleen, kidney and testes were also made. Hanging drop preparations were made after the improved method of Nemeczek 1926 for the study and measurement of fresh spores. For internal organs like liver, kidney, spleen and testes small pieces were cut, teased by means of dissecting needles after adding a drop of physiological saline and then examined. For the extrusion of polar filament 1 to 10% KOH solution was used. Lugol's iodine was used for studying the structure of the iodinophilous vacuole.

Smear preparations from the cysts and internal organs were fixed in Schaudinn's fluid and also in Carnoy's fixative. Delafield's and Heidenhains's haematoxylin stains were chiefly used for preparing permanent slides. Some of the smears were also subjected to Feulgen-nucleal reaction and Pyronin-Methyl green technique. Entire cysts were fixed in Bouin's fluid 6 μ thick sections were cut and stained in iron-alum-haematoxylin as well as Delafield's haematoxylin.

Results

The data collected during the course of investigation revels that the percentage of infection is highest with *Myxobolus punctatus* and lowest with *Unicauda bengalensis*. Table 1 shows the incidence of different parasites in *Ophicephalus punctatus*.

Table 1
Incidence of Myxosporidian parasite in *Ophicephalus punctatus* Bloch

Number of fishes		Myxosporidian parasites	Per cent of infection
examined	infected		
35	21	*Myxobolus punctatus* sp. n.	60
22	7	*Unicauda bicornuata* sp. n.	31.8
15	2	*Unicauda bengalensis* sp. n.	13.3

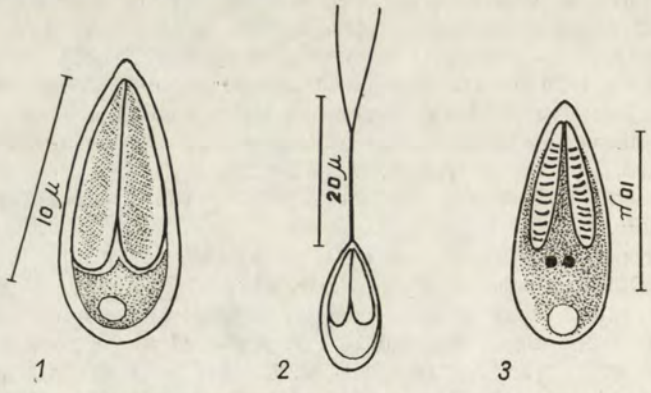
Myxobolus punctatus sp. n.

Seat to infection. Only in a single case, a few cysts were found attached to the pharyngeal epithelium whereas the spleen of all the infected fishes harboured the spores.

Locality. Calcutta and Naihati.

Cysts. The cysts are spherical or oval in shape and white in colour measuring about 1.0 to 1.3 mm in diameter. A well developed cysts membrane is present.

Spores. The spores are pyriform in shape with gradually pointed anterior and rounded posterior extremities. The polar capsules are situated at the anterior end and are equal in size. The tip of the capsules converge at the anterior end and a distinct polar filament is found to be coiled in each capsule. Granular sporoplasm fills the extra-capsular regions and has been found to be pyroninophilic (RNA). Two distinct round sporoplasmic nuclei are present lying close to each other. A large, more or less round iodinophilous vacuole is present below the nuclei of each mature spore (Figs. 1–3).



Figs. 1–3. Spores of *Myxobolus punctatus* sp. n. 1 — fresh spore showing iodinophilous vacuole, 2 — fresh spore after treatment with KOH solution, 3 — a stained spore

Table 2

Myxobolus punctatus sp. n. Dimensions of the spores in micron

	Range	Average
Length of the spore	12.29–15.0	14.45
Breadth of the spore	5.72–7.86	6.67
Length of the polar capsule	8.57–10.0	9.29
Breadth of the polar capsule	2.14–2.86	2.62
Length of the polar filament	42.25–32.56	35.78
Diameter of the iodinophilous vacuole		2.0

Unicauda bicornuata sp. n.

Seat of infection. Cysts were found attached mainly to the branchial epithelium and gills.

Locality. Calcutta.

Cysts. The cysts are oval in shape and milky white in colour measuring about 1.2 to 1.5 mm in diameter. A well developed cyst membrane is always present.

Spores. The main spore body is oblongate in shape, the anterior portion of which gradually ends in a rounded extremity. The posterior portion is gradually tapering and is continued into a long caudal prolongation. The caudal prolongation or process is single and undivided for a distance but is characteristically forked at its extreme end. Two equal sized polar capsules are situated at the anterior end of the spore. These are more or less pyriform in shape with their anterior tips approximated. A distinct ovate polar filament is present in each capsule. The extra-capsular region is filled with granular sporoplasm. Two distinct rounded nuclei which vary in their location, are present in the sporoplasm. The sporoplasm of each mature spore has a rounded iodinophilous vacuole in the posterior region below the nuclei (Fig. 4).

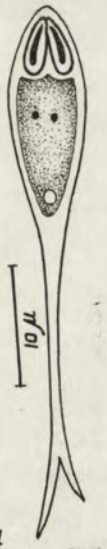


Fig. 4. A stained spore of *Unicauda bicornuata* sp. n. 4

Table 3

Unicauda bicornuata sp. n. Dimensions of the spores in micron

	Range	Average
Length of the spore (with caudal prolongation)	35.73–45.73	39.83
Length of caudal prolongation	14.29–27.15	21.54
Breadth of the spore	2.86– 4.29	4.02
Length of the polar capsule	6.0 – 7.15	6.54
Breadth of the polar capsule	1.43– 1.79	1.53
Length of the polar filament	26.83–35.64	30.5
Diameter of the iodinophilous vacuole		1.5

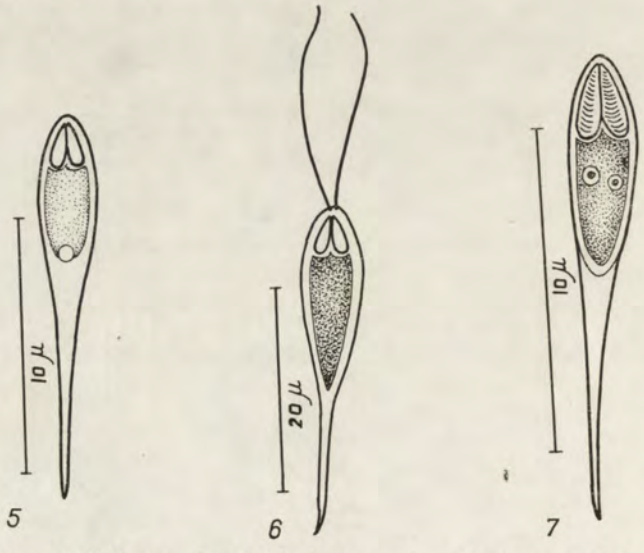
Unicauda bengalensis sp. n.

Seat of infection. Numerous cysts were found attached through the roof of the buccal cavity.

Locality. Naihati.

Cysts. The cysts are oval in shape and whitish in colour measuring about 1.0 to 1.25 mm in diameter. A well developed cyst membrane is always present (Pl. 1).

Spores. The spore body is oblongate in shape with gradually pointed anterior end. Posteriorly the main spore body is continued into a long caudal prolongation. This process is single and undivided through its length. Two pyriform polar capsules, with tips approximated are situated at the anterior end of the spore body and are equal in size. A distinct coiled polar filament is present within each capsule. Granular sporoplasm fills up the extra-capsular region. Two sporoplasmic nuclei which are distinct and round in appearance, usually lie close to one another. Below the nuclei of each mature spore is a rounded iodinophilous vacuole lying in the posterior region of the sporoplasm (Figs. 5–7).



Figs. 5–7. Spores of *Unicauda bengalensis* sp. n. 5 — fresh spore showing iodinophilous vacuole, 6 — fresh spore after treatment with KOH solution, 7 — a stained spore

Table 4

Unicauda bengalensis sp. n. Dimensions of the spores in micron

	Range	Average
Length of the spore (with caudal prolongation)	26.4–29.15	28.41
Length of the caudal prolongation	11.55–13.75	12.61
Breadth of the spore	2.75– 3.85	3.28
Length of the polar capsule	3.3 – 3.56	3.53
Breadth of the polar capsule	1.1 – 1.38	1.21
Length of the polar filament	18.0 – 27.0	21.75
Diameter of the iodinophilous vacuole		1.25

Discussion

Basing on the differences in host, size of the spores and polar capsules, fourteen species of *Myxobolus* have been described so far from the fresh water fishes of India.

Bhatt and Siddiqui 1964 reported for the first time two new species of *Myxobolus*, namely, *M. aligarhensis* and *M. ophicephali* from *Ophicephalus punctatus*. However, since Chakravarty 1939 already described *Henneguya ophicephali* from the same fish, Bhatt and Siddiqui's statement: "...constitute the first report of myxosporidian parasites from *Ophicephalus punctatus*" (p. 315) seems to be not tenable.

Myxobolus punctatus reported presently differs from the rest of the species of *Myxobolus* and also from *M. aligarhensis* and *M. ophicephali* in the shape and size of the spores, the position of the nuclei and iodinophilous vacuole and also in the shape of the polar capsules. On the basis of these differences *M. punctatus* is considered to be a new species.

Altogether fifteen species of *Unicauda* have so far been described of which only two are from the fresh water Indian teleosts.

Chakravarty 1939 reported *Henneguya ophicephali* from the gills and muscles of *Ophicephalus punctatus* with markedly different shape of spores in the two sites of infection. Chakravarty says "In the spores obtained from the gills, the tail was found bifurcated and devaricated" (p. 175). However, in the spores from the muscles the "bifurcations are approximated" (p. 175).

Davies 1944 divided the heterogenous genus *Henneguya*, family *Myxobolidae*, into three genera, basing primarily on the fundamental differences in the structure of the spores. One of these, the genus *Unicauda* was proposed for those species in which the spore has a single undivided posterior process.

Tripathy 1952 described *Unicauda ophicephali* from *Ophicephalus gachua* and regarded *Henneguya ophicephali* Chakravarty, 1939 to be synonymous (in part) with it. Tripathy's view was later endorsed by Bhatt and Siddiqui 1964. The present authors do not agree with Tripathy's view specially as regards the status of the forms described from the gills. Lalitha Kumari 1965 also expressed similar opinion.

Basing on the diagnostic characters of the genus *Unicauda* as proposed by Davies 1944, the two above described species can be placed under this genus. The main criteria for the establishment of new species have been based

on the differences in the host and spore characters, which still provide the only taxonomic basis for this group of parasites. *Unicauda bengalensis* differs from all the known species among the genus in the differences of measurements of spores and size of the polar capsules and *U. bicornuata* has a characteristic bifurcation at the tip of its caudal prolongation along with conspicuous differences in the spore dimensions.

Tripathy 1952 separated the existing species of *Unicauda* into three different groups basing on the size relationship between the caudal prolongation and the main body of the spore. But the view seems not tenable since large number of spores within the same cyst were obtained which were similar in all respects except in the length of the caudal prolongation. Bhatt and Siddiqui 1964 also did not support the grouping of the species of *Unicauda* as suggested by Tripathy 1952.

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Summary

Three new myxosporidian parasites infecting the common fresh water teleost *Ophicephalus punctatus* of Bengal (India) are discussed in detail. These are *Myxobolus punctatus* sp. n., *Unicauda bicornuata* sp. n., and *U. bengalensis* sp. n. The highest percentage of infection was observed with *Myxobolus punctatus* (60%), followed by *Unicauda bicornuata* (31.8%) and *U. bengalensis* (13.3%).

ZUSAMMENFASSUNG

Es wurden in allen Einzelheiten drei neue Myxosporidienparasite beschrieben, welche den *Ophicephalus punctatus*, einen gemeinen Knochenfisch der Binnengewässer von Bengal, infizieren. Es sind — *Myxobolus punctatus* sp. n., *Unicauda bicornuata* sp. n., und *U. bengalensis* sp. n. Der höchste Grad der Infektion wurde bei *Myxobolus punctatus* beobachtet (60%), nacher folgt *Unicauda bicornuata* (31.8%) und *U. bengalensis* (13.3%).

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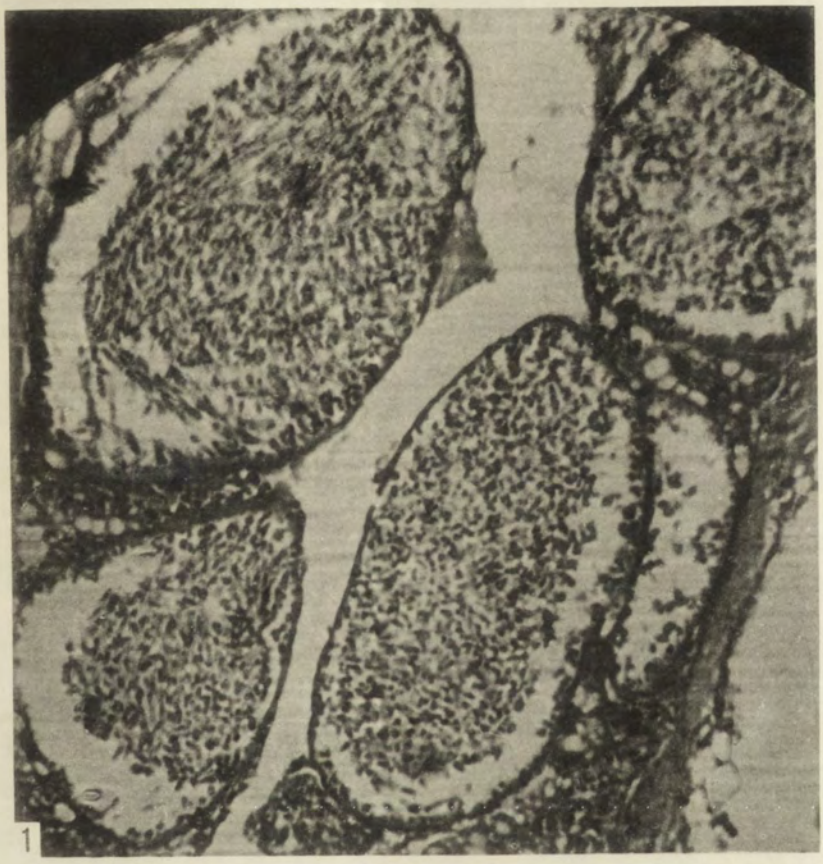
EXPLANATION OF PLATE I

Unicauda bengalensis sp. n.

1: Photomicrograph of the branchial epithelium of *Ophicephalus punctatus* showing several cysts with numerous spores within, 186 ×



S. Ray Chaudhuri et M. M. Chakravarty auctores phot.

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Parasites of the genus *Entamoeba*

Les parasites du genus *Entamoeba*

Genus *Entamoeba* comprises a group of parasitic amoebae. Excepting the free living *Entamoeba moshkovskii*, which occurs usually in sewage and pond they are found in the intestine of many vertebrates and several of them have been described from the invertebrates. Almost all the spontaneously occurring parasites described from the genus *Entamoeba* are endobiotic and of occasional nature. Their incidence varies to a large extent. *Schizomycetes* (Bacteria: *Micrococcus* and *Diplococcus*) and *Chytridiales* (Fungi: *Sphaerita* and *Nucleophaga*) have been described as spontaneous hyper-parasites from this genus of parasitic amoebae.

Breed et al. (1948, 1957) have compiled a comprehensive list of commensals and parasites of protozoa.

Schizomycetes

Micrococcus has been found in the cytoplasm of *E. muris* by Wenyon (1907). Because of the presence of a large number of healthy cocci of one kind, in one vacuole, it was suggested that the cocci have multiplied after being taken in by the amoeba. The author has concluded that the coccus in this case would be a parasite and might lead to the destruction of the amoeba.

Both the cytoplasm and nucleus of *E. minchini* (= *Loeschia hartmanni*) have been infected with micrococcus (MacKinnon 1914). She doubted that the nuclear parasite is micrococcus but believed it to be a developmental stage of *Nucleophaga*. Nöller (1922) has also reported bacterial attack ("diplokoken" = *Diplococci*) in the cytoplasm of *Entamoeba coli* cyst. This appears to be the first published account of the parasite of *Entamoeba* cyst. However, parasites of unknown systematic position, have been described from the cysts of *E. suis* (Ray and Das 1966 and Das and Ray 1968).

Chytridiales

Members of the order *Chytridiales* are mostly parasitic on plants and animals (Kirby 1941, also see Fitzpatric 1930, Minden 1915, and Sparrow 1960). Fungi of the two genera *Sphaerita* and *Nucleophaga* have been reported to parasitize the members of the genus *Entamoeba* and they are discussed below.

Sphaerita

It has been reported from all the species of intestinal amoebae of man. Within the scope of this review *Sphaerita* parasites of the genus *Entamoeba* only will be considered.

Entamoeba histolytica (Bacigalupo 1927, 1928; Greenway 1926; Lwoff 1925; Nöller 1921) and *E. coli* (Bacigalupo 1927, 1928; Cragg

1919, Epstejn 1922, 1931; Lwoff 1925 and Nöller 1921) have been reported to harbour the *Sphaerita* in their cytoplasm. Lwoff (1925) considered that the parasites of *E. histolytica* (= *E. dysenteriae*) and *E. coli* (also of *Endolimax nana*) are identical with *Sphaerita endogena*, but he gave the new name — *Sphaerita normanti* provisionally with the hope that it might be proved to be a new species of hyperparasite. Brumpt and Lavier (1935) have also reported *Sphaerita* from *E. histolytica* (= *E. disper*).

Entamoeba salpae of marine fishes, *Box boops* [= *Boops boops*][1] and possibly *Box salpa* [= *Salpa salpa*] has been found to be often parasitized by microspheres (Léger et Duboscq 1904) which Kirby (1941, p. 1045) has considered as chytrids. Further work on this hyperparasite will disclose its real identity. Carini (1944) and Neal (1953) have described *Sphaerita* in *E. testudinia* and *E. moshkovskii* respectively.

Kessel (1924) and Neal (1950) have reported *Sphaerita* from *E. muris*. *Sphaerita endamoeba* has been described from *Entamoeba citelli* of *Citellus tridecemlineatus* [=*Citellus tridecemlineatus tridecemlineatus*], striped ground squirrel from Iowa, USA, by Becker (1926). The same chytrid has also been described by Zasukhin (1931) and Zasukhin et al. (1930) from the same species of *Entamoeba* of *Citellus pygmaeus* (Pallus) of South East Russia.

Further reports of *Sphaerita* are from *E. bobaci* of *Marmota bobac* [= *Marmota bobak*] (Yuan-Po 1928), *E. pitheci* from *Macacus rhesus* [= *Macaca mulatta*] (Zasukhin et al. 1930), and *Entamoeba* sp. of cattle (Jirovec 1933). A third degree parasitism has been observed in the *Sphaerita* of *Entamoeba paulista* which is harboured by *Zelleriella*, the *Opalinid protozoa*, parasitic in the intestine of anurans (Stabler and Chen 1936).

Table 1

Degree of incidence of *Sphaerita* in *Entamoeba*, where it is clearly stated

Sl. No.	Species	Remarks	Reference
1.	*E. coli*	A very high percentage infected	Nöller 1921
2.	*E. coli*	80 per cent	Lwoff 1925
3.	*E. histolytica*		
4.	*E. citelli* from ground squirrels of USA	Very high	Becker 1926
5.	*E. bobaci*	60 per cent	Yuan-Po 1928
6.	*E. citelli* from Russian "steppe suslik"	Very heavy	Zasukhin et al. 1930 Zasukhin 1934
7.	*E. moshkovskii*	A few	Neal 1953

Nucleophaga

The parasites are found in the nucleus of many entozoic amoebae. Lavier (1935 b) has reviewed some of these accounts. Zasukhin (1931) has found them in the nucleus of *Entamoeba citelli*, of *Citellus pygmaeus* from South

[1] Modern names of the hosts, where necessary, are given in the third bracket.

Table 2

Parasites of *Entamoeba*

First host	Second host	Third host	*Schizomycetes* (Bacteria)		*Chytridiales* (Fungi)		References
			Micrococcus	*Diplococcus*	*Sphaerita*	*Nucleophaga*	
Entamoeba sp.	Cattle				+		a
E. bobaci	*Marmota bobac* [= *Marmota bobak*]				+		b
E. citelli	*Citellus tridecemlineatus* [= *C. tridecemlineatus tridecemlineatus*] *C. pygmaeus*				+	+	c
E. coli	*Homo sapiens*			+	+	?+	d
E. hartmanni	*Homo sapiens*				+		e
E. histolytica	*Homo sapiens*				+		f
E. minchini	*Tipula* sp. larvae		+			+	g
E. moshkovskii	So far free-living, found in a Sewage near London				+		h
E. muris	Rats				+	+	i
E. paulista	*Zelleriella* sp.	*Pleurodema bibroni* and *Bufo marinus*			+		j
E. pithici	*Macacus rhesus* [= *Macaca mulatta*]				+		k
E. ranarum	*Alytes obstetricans*					+	l
E. salpae	*Box boops* [= *Boops boops*]				+		m n
E. testudinia	*Testudo tabulata* [= *Testudo denticulata*]				+		o
E. suis	Indian domestic pig, *Sus scrofa*		An unidentified hyperparasite in the cyst cytoplasm				

References to Table 2.

a. Jirovec (1933). b. Yuan-Po (1928). c. For *Sphaerita* see Becker (1926) and Zasukhin et al. (1930) and for *Nucleophaga* see Zasukhin (1931). d. For *Diplococcus* see Nöller (1922) and for *Sphaerita* see Bacigalupo (1927, 1928); Cragg (1919); Nöller (1921); Epstejn (1922, 1931, 1941); Lwoff (1925). For a nuclear parasite of doubtful systematic position see Casagrandi and Barbagallo (1987), and Epstejn (1931, p. 125). e. Brumpt el Lavier (1935). f. Bacigalupo (1927, 1928); Greenway (1926); Lwoff (1925); Nöller (1921). g. MacKinnon (1914). h. Neal (1953). i. For *Sphaerita* see Kessel (1924); Neal (1950, p. 346); Wenrich (1940); Wenyon (1907). For *Nucleophaga* see Wenrich (1940, description p. 218, pl. 1. Fig. 5 of p. 233). j. Stabler and Chen (1936). k. Zasukhin et al. (1930). l. Lavier (1935 a, b). m. Léger and Duboscq (1904). n. Carini (1944). o. Ray and Das (1966) and Das and Ray (1968).

East Russia. Vickerman (1960) found it in the nuclei of *E. minchini* of *Tipula* larvae collected from South West England. *Nucleophaga ranarum* has been described from the nucleus of *E. ranarum* by Lavier (1935 b). Wenrich (1940) has also reported nuclear parasites of *E. muris* as a nucleophaga-like inclusion in the periendosomal region. The real nature of the hyperparasite remains to be ascertained.

Although much remains to be done on the life history, morphology, and taxonomy of the hyper-parasites of the genus *Entamoeba*, they are not discussed in the present review. However, Epstejn (1941, p. 128–129) believed that the cytoplasmic and nuclear fungi which do not produce sporangia are different from the others. He evidently intends to create new genera of *"Plasmapthora"* and *"Nucleopthora"* for the cytoplasmic and nuclear fungi, respectively of the parasitic amoebae. He was also aware of the difficulty in separating these two groups of hyperparasites.

Parasites of uncertain nature

In the nucleus of *Entamoeba coli* Casagrandi and Barbagallo 1897 described small, rounded bodies, equal in size, and sometimes so numerous as to fill the whole of the nucleus. These bodies were suggested by Cragg (1919) as parasites possibly *Sphaerita*, and not nuclear parasites. Kirby (1941, p. 1044) has endorsed this and put forward the view that Craig (1911, Fig. 8, adapted from Casagrandi and Barbagallo 1897) was possibly dealing with *Sphaerita* in *E. coli*. Further evidence of cytoplasmic parasites of *E. coli* has come from Epstejn (1931, Figs. 145 and 211 e; 1941, pl. 33, Figs. 3, 5, 6; pl. 41, Fig. 12). He has called them *"Plasmapthora"* but their real nature still requires investigation.

Ivanic (1936) found a parasite in *E. histolytica*. He called it *Entamoebophaga hominis* and claimed its affinity with mycetozoa. Because of the Ivanic's description of the hyperparasite is difficult to understand, Kirby (1941, p. 1078) has justifiably doubted this.

An unidentified hyperparasite in the cysts of *E. suis* from Indian domestic pig, *Sus scrofa* has been described by Ray and Das (1966) and Das and Ray (1968).

Host specificity

Yuan-Po (1928) has suggested that more than one species of *Sphaerita* may be found in *Entamoeba*. Host specificity has been suggested by Brumpt and Lavier (1935). They observed two different species of hyper-parasites in two different species of amoebae on the same smear. *Sphaerita parvula* was found in *Hyalolimax cercopitheci* (pl. 14, Figs. 21, 22) and large spore bearers in *E. hartmanni* (= *Entamoeba minuta*, pl. 14, Fig. 24).

While studying *Nucleophaga* in *Endolimax nana*, Brumpt and Lavier (1935) observed *Sphaerita* in the cytoplasm of a few *E. histolytica* (= *E. disper*, Fig. 12). Neither the cytoplasm of *Endolimax nana*, (nuclei of which were mostly ravaged with *Nucleophaga*), nor the nuclei of *E. histolytica* (= *E. disper*) (a few of which contained *Sphaerita* in their cytoplasm), were invaded by the hyperparasites; although the material was from the some source. Based on these observations they suggested host specificity in these hyperparasites. Opposite wiews are favoured by Lwoff (1925) and Kirby (1941).

Effects of hyperparasites on *Entamoeba*

Very little is known about the real relationship of these parasites with the host *Entamoeba*. Many protozoa infected with *Sphaerita*, may appear to be normal although occasionally they could succumb. Perusal of literature indicates that the host protozoa may get rid of their parasites and return to their normal mode af life. During sporulation of the hyperparasite, death of the host protozoa has also been noticed.

Becker (1926) has described degenerative changes particularly in the nucleus of *E. citelli* from *Citellus tridecemlineatus* [= *Citellus tridecemlineatus tridecemlineatus*] due to *Sphaerita*. Similar changes have also been recorded from the same species of *Entamoeba* from *Citellus pygmaeus* ("steppe suslik" of USSR) by Zasukhin (1933, 1934). Further, Zasukhin pointed out that the growth of *Sphaerita* initially hampers the metabolism of the host *Entamoeba* and ultimately destroys it. Incidence of large numbers of *Sphaerita* in *E. citelli* led Zasukhin (op. cit) to suggest that this *Entamoeba* may possibly be exterminated some day by the hyperparasite. MacKinnon (1914) also described degeneration of *E. minchini* due to the nuclear parasite. Yuan-Po (1928) has reported death of *E. bobaci* when the sporangiam of *Sphaerita* within it ruptures or is about to do so. Epstejn's (1922, p. 64) Fig. 5 of *E. coli* also suggests this phenomenon.

An unidentified hyperparasite in the cytoplasm of *E. suis* cyst collected from Indian domestic pig, *Sus scrofa*, appeared to have interferred the synthesis of DNA and RNA of the host amoeba (Das and Ray, 1968). The structural changes found in the parasitized *E. suis* cysts, appeared to have rendered them non-viable (Ray and Das 1966). Further work would disclose the identity of the hyperparasite and its ultimate effect on the viability of the *E. suis* cysts.

Summary and conclusion

So far, fifteen species of *Entamoeba* have been reported to harbour hyperparasites either in the cytoplasm or in the nucleus. In most cases trophozoites are usually involved and it is likely that these hyperparasites interfere with the normal functions of the host amoebae.

Presence of hyperparasites in the amoebae may be of considerable interest and importance. Should these hyperparasites have any cytopathogenic effect on the amoebae or interfere directly or indirectly with their morphogenesis or growth, the question of taking advantage of hyperparasitism in the biological control of these amoebae would seem to deserve critical consideration. Needless to mention, factors involved in the natural control and regulation of parasite population are yet to be known. However, before the concept of biological control is entertained, further studies will be necessary to disclose different facets of this host-parasite relationship viz., source of these hyperparasites, their mode and frequency of invasion, extent of colonization, pathogenic potential and the prospect and degree of certainty with which hyperparasitism can be experimentally induced.

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RESUME

Jusqu' à maintenant on a constanté que 15 espèces du *Entamoeba* ont des hyperparasites la cytoplasme ou bien dans le nucléus. Dans la majorité des cas il s'agit des trophozoites et il est possible que ces hyperparasites nuisant aux fonctions normales de l'Amibe-hôte.

La presence des hyperparasites chez les Amibes peut être hautement significative. Si les hyperparasites avaient un effet cytopathogène sur l'Amibe ou bien bloquaient directement ou indirectement leur morphogenèse ou croissance on devrait considerer sérieusement le problème du hyperparasitisme comme moyen du contrôle biologique de ces Amibes. Il est inutile de dire que les facteurs prenant part dans le contrôle naturel et regulation de la population des parasites ne sont pas connus encore. Mais avant que l'idée du controle biologique soit considerée des études suivantes seront necessaires pour eclaircir les aspects differents de cette relation hôte-parasite, c'est à dire la source de ces hyperparasites, leur mode et frequence d'invasion, le degré de colonisation, le potentiel pathogène et le degré de probabilité et la possibilité avec laquelle le hyperparasitisme pourrait être induqué.

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Инфузории песчаной литорали и сублиторали Кандалакшского залива (Белое море) и анализ данных по фауне бентосных инфузорий других морей

Ciliates of the sand littoral and sublittoral of Kandalaksha Gulf (White Sea) and the analysis on the fauna of benthic ciliates of other seas

В настоящей работе приводятся дополнительные сведения по фауне и экологии бентосных инфузорий Белого моря (ранее изучавшиеся Мережковским 1878, Броцкой 1951 и Райковым 1962), анализируется родовой и видовой состав инфузорий различных морских водоёмов, а также обсуждается вопрос о географическом распространении морских бентосных инфузорий.

Автор пользуется случаем выразить глубокую благодарность своим руководителям профессору Л. А. Зенкевичу и сотруднику кафедры О. И. Чибисовой за постоянную помощь в работе.

Методы исследования

Исследование проводилось летом и осенью 1964–1969 гг. и зимой 1967 года. Применялись как общепринятые методы сбора микробентоса, так и некоторые приспособления собственной конструкции (например, поршневая трубка с многочисленными отводами на разных уровнях для одновременного сбора грунта, детрита и придонной воды). Большая часть проб была собрана на литорали или на границе литорали и сублиторали, значительно меньшая часть — в сублиторали, с глубины до 40 метров. В общей сложности обработано свыше 1100 образцов грунта, детрита и придонной воды. Кроме того изучалось население других местообитаний (водорослевый ил, поверхность непористых субстратов, скопления живых нитчатых водорослей, наскальные заплески и др.). Определение инфузорий велось на живом и фиксированном материале, импрегнированном серебром (по Chatton et Lwoff) или окрашенном гемалауном, или другими ядерными красителями. При определении инфузорий пользовались монографией Каля (Kahl 1930–1935) и позднейшими описаниями.

Особенности гидрометеорологического режима Белого моря

Белое море, в современных его границах, является молодым полуконтинентальным водоёмом, сообщающимся узким проливом с Баренцевым морем и океаном. В геологически недалёком прошлом (6–7 тысяч лет тому назад) оно сооб-

щалось также с Балтийским морем. Объём Белого моря не превышает 1/250 000 части объёма Мирового океана (Зенкевич 1963).

В целом водоём характеризуется суровым гидрометеорологическим режимом. Средняя годовая температура воды за несколько последних десятилетий не превышает 4°С. Большую часть года Белое море покрыто льдом. Зимой температура воды отрицательная (−1.4°С). Такая же температура сохраняется летом на глубинах ниже 50–100 метров. Летом на мелководиях вода прогревается до 20°С, а грунт на осушенной литорали иногда до 32°С. На литорали наблюдаются резкие суточные колебания температуры грунта (Бурковский 1968 b).

Из-за мощного материкового стока (1/77 часть мирового стока) солёность Белого моря значительно ниже океанической и составляет в среднем 25–26.5‰. В отдельные периоды года на осушенной литорали солёность грунтового раствора понижается до 5–10‰. В целом солёность грунтового раствора на 2–4‰ выше солёности окружающей воды.

На глубинах ниже 40–50 метров ощущается недостаток кислорода.

Типы грунтов

Грунты прибрежной зоны чрезвычайно разнообразны по механическим свойствам и по количеству заключённых в них органических веществ. Как правило, верхний горизонт литорали представлен мелким гравием (1–3 мм), крупнозернистым (0.5–1.0 мм) или среднезернистым песком (0.25–0.50 мм) с небольшим количеством органических веществ (0.2–0.4% от веса осадка). Средний и нижний горизонты литорали, а также сублитораль (за исключением мест с сильным придонным течением) заняты мелким гетерогенным (0–0.25 мм) или мелким гомогенным (0.1–0.2 мм) песком со средним или высоким содержанием органических веществ (0.6–1.6% от веса осадка). Кроме того в прибрежной зоне распространены илистые и глинистые грунты, почти не содержащие инфузорий.

Экологический анализ инфузорий песчаной литорали и сублиторали Белого моря

В целом нами было отмечено 210 видов, из которых 135 видов не были раньше известны для Белого моря. 17 видов описаны в предыдущих работах как новые для науки (Бурковский 1970 a, b). Учитывая дополнительные данные Мережковского (1878) и Райкова (1962), фауна инфузорий микробентоса Белого моря составляет 219 видов.

В бентосе Белого моря нами обнаружены 8 пресноводных и 18 солоноватоводных инфузорий, которые вместе составляют 15% от общего числа известных для этого моря бентосных инфузорий. Пресноводные инфузории *Kahliella costata*, *Perispira stephosoma*, *Lacrymaria metabolica*, *Loxophyllum niemeccense* встречаются редко и в небольшом количестве. Можно предположить их случайное проникновение в морской песок вместе с токами пресной воды. Другие пресноводные инфузории *Strombidium viride*, *Hemiophrys fusidens*, *Microthorax sulcatus*, *Leptopharynx torpens* — постоянные обитатели морского песка. Последний вид встречается в сублиторали. Особи всех перечисленных видов морфологически неотличимы от особей, встречающихся в их типичных условиях. Некоторые из пресноводных и почти все солоноватоводные инфузории встречались ранее и в других морях.

В Таблице 1 приводятся общие сведения о распределении и встречаемости инфузорий, обнаруженных нами в морском песке.

Таблица 1
Table 1

Распределение морских бентосных инфузорий по биотопам
Biotopic distribution of the marine benthic ciliates

Вид инфузорий Species of ciliates	Придонная вода Near-bottom water	Детрит* Detrite*	Поверхность субстрата** Surface of substrate**	Песок (интерстициаль) Sand (interstitial)				
				0.1–0.2 mm	0–0.25 mm	0.25–0.50 mm	0.5–1.0 mm	1–3 mm
1	2	3	4	5	6	7	8	9
Subclasis *Holotricha* Stein								
Ordo *Gymnostomatida* Bütschli								
Subordo *Rhabdophorina* Fauré-Fremiet								
Familia *Enchelyidae* Ehrenberg								
1. *Urotricha biconica* Sauerbey	1***	1	—	—	1	1	—	—
2. *Prorodon discolor* Ehrenberg	1	2	—	1	2	—	—	—
3. *P. teres* Ehrenberg	1	1	—	—	1	3	3	1
4. *P. morgani* Kahl	1	1	—	—	—	1	2	—
5. *P. moebiusi* Kahl	1	2	—	—	—	2	2	1
6. *P. binucleatus* Buddenbrock	1	1	—	—	1	1	—	—
7. *P. dubius* Kahl	—	2	—	—	1	—	—	—
8. *P. marinus* Fauré-Fremiet	1	1	—	1	1	1	—	—
9. *Prorodon* sp.	1	2	—	—	1	2	1	—
10. *Pseudoprorodon arenicola* Kahl	—	—	—	2	2	—	—	—
11. *P. mononucleatum* Bock	—	—	—	1	1	—	—	—
12. *Helicoprorodon gigas* Kahl	—	—	—	1	1	—	—	—
13. *Helicoprorodon* sp.	—	—	—	1	1	—	—	—
14. *Plagiopogon loricatus* Kahl	1	2	—	—	1	2	2	—
15. *Placus striatus* Cohn	1	1	—	—	—	2	3	1
16. *P. dogieli* Burkovsky	1	1	—	—	1	3	3	1
17. *Lagynophrya halophila* Kahl	1	1	—	1	2	2	2	1
18. *L. maxima* Burkovsky	1	—	—	—	1	1	—	—
19. *Lacrymaria cohni* Kent	—	1	—	1	2	1	—	—
20. *L. lagenula* Clap. et Lachm.	—	—	—	—	—	1	—	—
21. *L. coronata* Clap. et Lachm.	1	1	—	—	1	2	2	1
22. *L. marina* Kahl	1	3	—	2	3	2	1	1
23. *L. caudata* Kahl	—	—	—	—	1	2	1	1
24. *L. minima* Kahl	—	2	—	—	—	—	1	—
25. *L. salinarum* Kahl	—	2	—	—	1	1	—	—
26. *L. metabolica* Bürger	—	1	—	—	—	1	—	—
27. *L. ovata* Burkovsky	—	2	—	—	1	1	1	—
28. *L. conifera* Burkovsky	1	2	—	1	2	2	1	—
29. *Chaenea elongata* Maupas	—	1	—	1	—	—	—	—

1	2	3	4	5	6	7	8	9
30. *Ch. robusta* Kahl	1	2	—	—	—	1	2	1
31. *Trachelophyllum apiculatum* Perty	—	—	—	—	1	—		—
Familia *Colepidae* Ehrenberg								
32. *Coleps pulcher* Spiegel	1	1	—	—	—	2	3	2
33. *C. tesselatus* Kahl	1	2	—	—	—	2	3	2
34. *C. similis* Kahl	1	2	—	—	—	3	3	2
35. *C. spiralis* Noland	1	2	—	—	—	2	1	—
Familia *Trachelocercidae* Kent								
36. *Trachelocerca minor* Gruber	—	—	—	1	1	—	—	—
37. *Tc. tenuicollis* Quennerstedt	—	—	—	1	1	1	—	—
38. *Tc. coluber* Kahl	—	—	—	1	2	—	—	—
39. *Tc. schulzei* Dragesco	—	—	—	1	1	—	—	—
40. *Trachelor aphis drachi* Dragesco	—	—	—	1	2	—	—	—
41. *Tr. drachi* var. *bimicronucleata* Raikov	—	1	—	2	3	1	—	—
42. *Tr. kahli* Raikov	—	—	—	2	2	—	—	—
43. *Tr. prenanti* Dragesco	—	—	—	1	1	—	—	—
44. *Tr. margaritatus* Kahl	—	—	—	1	1	—	—	—
45. *Tr. phoenicopterus* Cohn	1	2	—	3	4	2	1	—
46. *Tr. striatus* Raikov	—	1	—	2	3	1	—	—
47. *Tr. dogieli* Raikov	—	—	—	1	—	—	—	—
48. *Tr. teissieri* Dragesco	—	—	—	—	1	—	—	—
49. *Tr. discolor* Raikov	—	—	—	1	—	—	—	—
50. *Tr. incaudatus* Kahl	—	2	—	2	3	1	—	—
51. *Tr. vermiformis* Raikov	—	—	—	—	1	—	—	—
52. *Trachelonema grassei* Dragesco	—	—	—	1	1	—	—	—
53. *Tn. longicollis* Dragesco	—	—	—	1	1	—	—	—
54. *Tn. oligostriata* Raikov	1	2	—	2	3	1	—	—
55. *Tn. lanceolata* Raikov	—	—	—	1	1	—	—	—
Familie *Didiniidae* Poche								
56. *Mesodinium pulex* Clap. et Lachm.	3	2	—	2	2	3	3	1
57. *M. pulex* var. *pupula* Kahl	3	1	—	1	2	3	2	1
58. *Didinium balbiani* var. *nanum* Kahl	2	—	—	1	1	1	—	—
59. *Askenasia stellaris* Leegard	2	—	—	—	1	1	1	—
60. *Cyclotrichium cyclocaryon* Meunier	2	—	—	—	—	1	1	—
61. *C. sphaericum* Fauré-Fremiet	4	—	—	—	—	1	2	2
Familia *Spathidiidae* Kahl								
62. *Spathidium curvatum* Kahl	—	—	—	2	—	—	—	—
63. *Paraspathidium fuscum* Kahl	—	—	—	2	3	1	—	—
64. *P. obliquum Dragesco*	—	—	—	2	2	—	—	—
65. *Perispira stephosoma* Stokes	2	2	—	—	1	1	—	—
Familia *Amphileptidae* Bütschli								
66. *Hemiophrys filum* Gruber	—	1	—	2	2	1	—	—
67. *H. fusidens* Kahl	—	1	—	1	2	1	—	—
68. *H. salmica* Burkovsky	—	2	—	—	—	2	3	—

1	2	3	4	5	6	7	8	9
69. *Litonotus lamella* Ehrenberg	—	2	—	—	1	1	1	—
70. *L. pictus* var. *binucleatus* Kahl	—	—	—	—	2	2	1	—
71. *L. anguila* Kahl	—	1	—	1	2	2	2	—
72. *L. fasciolatus* Dragesco	—	1	—	1	2	2	2	1
73. *Litonotus* sp.	—	—	—	—	1	—	—	—
74. *Loxophyllum variabilis* (?) Dragesco	—	1	—	—	1	2	2	1
75. *L. multiplicatum* Kahl	—	2	—	—	1	1	1	—
76. *L. soliforme* Fauré-Fremiet	—	1	—	—	—	1	1	—
77. *L. undulatum* Sauerbrey	—	—	—	—	—	1	1	—
78. *L. uninucleatum* Kahl	—	—	—	—	—	1	—	—
79. *L. levigatum* Sauerbrey	—	—	—	—	—	3	2	1
80. *L. trinucleatum* Manfeld	—	1	—	—	—	1	—	—
81. *L. niemeccense* Stein	—	—	—	—	—	1	—	—
82. *L. helus* Stokes	—	—	—	—	1	1	1	—
83. *L. helus* var. *rotundatum* Florentin	—	2	—	—	—	2	1	—
84. *L. vermiforme* Sauerbrey	—	—	—	—	—	1	1	—
85. *L. asetosum* Burkovsky	—	1	—	—	—	2	2	—
86. *L. schewiakoffi* Burkovsky	—	—	—	—	1	—	—	—
Familia *Loxodidae* Bütschli								
87. *Remanella rugosa* Kahl	—	1	—	2	3	1	—	—
88. *R. unicorpusculata* Kahl	—	1	—	2	2	—	—	—
89. *R. granulosa* Kahl	—	1	—	3	2	1	—	—
90. *R. margaritifera* Kahl	1	2	—	3	4	2	1	—
91. *Remanella* sp.	—	—	—	—	—	—	—	—
92. *Kentrophoros fasciolatum* Sauerbrey	—	1	—	2	2	1	—	—
93. *K. latum* Raikov	—	—	—	1	1	—	—	—
94. *K. grandis* Dragesco	—	—	—	1	1	—	—	—
95. *K. gracile* Raikov	—	—	—	1	1	—	—	—
96. *K. uninucleatum* Raikov	—	—	—	—	1	—	—	—
Subordo *Cyrtophorina* Fauré-Fremiet								
Familia *Chlamydodontidae* Claus								
97. *Chlamydodon triquetrus* O. F. M.	—	2	—	1	2	2	1	—
98. *Ch. triquetrus* var. *major* Kahl	—	1	1	—	2	—	—	—
99. *Ch. obliquus* Kahl	—	1	—	—	—	1	1	—
100. *Ch. cyclops* Entz	—	1	—	1	3	2	1	1
101. *Ch. mnemosyne* Ehrenberg	—	1	1	—	2	1	—	—
102. *Cryptopharynx setigerus* Kahl	—	1	—	—	1	—	—	—
103. *Chilodonella* sp.	—	—	—	—	1	—	—	—
Familia *Nassulidae* Bütschli								
104. *Chilodontopsis vorax* (?) Stokes	—	2	—	—	2	—	—	—
Familia *Dysteriidae* Clap. et Lachm.								
105. *Dysteria monostyla* Ehr–Stein	—	3	1	—	1	—	—	—
Ordo *Trichostomatida* Bütschli								
Familia *Coelosomididae* Corliss								
106. *Coelosomides vermiformis* Burkovsky	—	—	—	—	—	1	3	1

1	2	3	4	5	6	7	8	9
Familia *Plagiopylidae* Schewiakoff								
107. *Plagiopyla ovata* Kahl	1	2	—	—	—	2	3	1
108. *P. marina* Kahl	—	1	—	—	—	2	2	—
Familia *Geleiidae* Kahl								
109. *Geleia murmanica* Raikov	—	—	—	—	1	1	—	—
110. *G. fossata* Kahl	—	—	—	1	2	—	—	—
111. *G. nigriceps* Kahl	—	—	—	1	2	—	—	—
112. *G. decolor* Kahl	—	—	—	1	2	—	—	—
113. *G. orbis* Fauré-Fremiet	—	—	—	—	1	—	—	—
114. *G. hyalina* Dragesco	—	1	—	2	3	1	—	—
115. *G. simplex* Fauré-Fremiet	—	—	—	—	1	—	—	—
116. *Geleia* sp.	—	—	—	1	1	—	—	—
Familia *Leptopharyngidae* Kahl								
117. *Leptopharynx torpens* Kahl	—	—	—	—	—	2	1	—
118. *Microthorax sulcatus* Engelmann	—	—	—	—	—	2	2	—
Ordo *Hymenostomatida* Del. et Hér.								
Subordo *Tetrahymenina* Fauré-Fremiet								
Familia *Uronematidae* Thompson								
119. *Uronema marinum* Dujardin	1	2	—	1	2	1	1	—
Familia *Philasteridae* Kahl								
120. *Helicostoma notatum* Möbius	1	2	—	1	3	2	1	—
121. *H. buddenbrocki* Kahl	1	2	—	1	2	1	—	—
122. *Philaster* sp.	1	1	—	1	2	2	—	—
Subordo *Peniculina* Fauré-Fremiet								
Familia *Frontoniidae* Kahl								
123. *Frontonia microstomata* Kahl	—	—	—	—	1	—	—	—
124. *F. arenaria* Kahl	—	1	—	1	2	1	—	—
125. *F. fusca* Quennerstedt	1	2	—	1	2	1	—	—
126. *F. maris-albi* Burkovsky	1	2	—	2	3	2	2	1
127. *F. tchibisovae* Burkovsky	1	1	—	—	2	3	3	1
128. *F. elongata* Burkovsky	—	1	—	1	2	1	—	—
129. *Cardiostomella vermiforme* Kahl	1	2	—	2	3	2	1	—
130. *Cardiostomella* sp.	—	1	—	2	2	—	—	—
Familia *Ophryoglenidae* Kent								
131. *Ophryoglena macrostomata* Kahl	1	1	—	1	1	—	—	—
132. *O. marina* Burkovsky	2	1	—	1	2	2	1	—
Subordo *Pleuronematina* Fauré-Fremiet								
Familia *Pleuronematidae* Kent								
133. *Cyclidium velliferum* Kahl	1	3	—	1	2	2	1	1
134. *C. candens* Kahl	—	1	—	—	1	—	—	—
135. *Cyclidium* sp.	1	2	—	1	2	1	1	—
136. *Cristigera setosa* Kahl	1	3	—	1	2	2	2	1
137. *Cristigera* sp.								
138. *Pleuronema coronatum* Kent	2	4	—	2	3	3	3	2

1	2	3	4	5	6	7	8	9
139. *P. marinum* Calkins	1	2	—	1	2	1	—	—
140. *P. setigerum* Calkins	1	2	—	2	2	1	1	1
141. *P. simplex* Dragesco	1	2	—	1	1	1	—	—
142. *Histiobalantium* marinum Kahl	1	3	—	1	2	2	—	—
143. *H. majus* Kahl	—	3	—	1	3	2	1	—
Subclassis *Spirotricha* Bütschli								
Ordo *Heterotrichida* Stein								
Familia *Peritromidae* Stein								
144. *Petritromus faurei* Kahl	—	1	—	—	1	—	—	—
Familia *Spirostomatidae* Stein								
145. *Blepharisma salinarum* Florentin	—	—	—	—	2	—	—	—
146. *B. clarissimum* Anigstein	—	1	—	2	2	—	—	—
147. *B. clarissimum* var. *arenicola* Kahl	—	1	—	2	2	1	—	—
148. *Gruberia uninucleata* Kahl	—	—	—	1	1	—	—	—
149. *G. lanceolata* Gruber	—	—	—	1	1	—	—	—
150. *Gruberia* sp.	—	—	—	—	1	—	—	—
Familia *Condylostomatidae* Kahl								
151. *Condylostoma arenarium* Spiegel	—	2	—	—	1	1	—	—
152. *C. remanei* Kahl	—	1	—	2	2	1	—	—
153. *C. patens* O. F. M.	—	2	—	1	2	1	—	—
154. *C. curva* Burkovsky	—	2	—	1	2	2	1	—
155. *Condylostoma* sp.	—	—	—	—	1	—	—	—
Ordo *Oligotrichida* Bütschli								
Familia *Halteriidae* Clap. et Lachm.								
156. *Strombidium sauerbreyae* Kahl	3	1	—	2	2	3	1	—
157. *S. sulcatum* Clap. et Lachm.	4	2	—	2	3	4	3	2
158. *S. viride* Clap. et Lachm.	2	—	—	1	1	2	1	—
159. *S. typicum* Bütschli	1	—	—	—	—	1	—	—
160. *S. calkinsi* Kahl	2	1	—	—	—	2	2	—
161. *Strombidium* sp.	2	—	—	—	—	1	—	—
Ordo *Tintinnida* Clap. et Lachm.								
162. *Tintinopsis karajacensis* Brandt	3	1	—	1	2	2	1	—
163. *Helicostomella subulata* Jörgensen	2	—	—	—	1	1	—	—
164. *Parafavella denticulata* Kof. et Campb.	2	—	—	—	1	1	—	—
165. *Favella* sp.	2	—	—	—	1	—	—	—
Ordo *Hypotrichida* Stein								
Familia *Oxytrichidae* Ehrenberg								
166. *Epiclintes ambiquus* O. F. M.	—	1	—	1	3	1	—	—
167. *Kahliella costata* Kahl	—	—	—	—	—	1	—	—
168. *Urostrongylum caudatum* Kahl	—	—	—	1	1	—	—	—
169. *Keronopsis multinucleatum* Maupas	—	—	—	—	1	—	—	—
170. *K. rubra* Ehrenberg	—	—	1	2	2	1	—	—
171. *Keronopsis* sp.	—	—	2	1	1	2	—	1
172. *Holosticha kessleri* Wrzes.	—	1	2	1	2	2	1	—

1	2	3	4	5	6	7	8	9
173. *H. manca* Kahl	—	—	1	—	1	2	1	—
174. *H. diademata* Pees	—	1	2	1	2	3	2	1
175. *H. simplicis* (?) Wang. et Nie	—	—	1	—	2	1	1	—
176. *H. discocephalus* Kahl	—	—	—	—	1	—	—	—
177. *H. fasciola* Kahl	—	—	—	1	1	—	—	—
178. *Amphisiella milnei* Kahl	—	1	1	—	1	1	—	—
179. *Amphisiella* sp.	—	—	1	1	1	—	—	—
180. *Trichotaxis multinucleatus* Burkovsky	—	—	1	2	2	1	1	—
181. *Trachelostyla pediculiformis* Cohn	—	2	2	2	3	3	2	1
182. *T. caudata* Kahl	—	2	2	1	2	2	—	—
183. *Gastrostyla pulchra* Perejaslawzewa	—	2	2	1	3	3	2	1
184. *Oxytricha discifera* Kahl	—	1	—	—	1	1	—	—
185. *Oxytricha* sp.	—	—	1	—	—	1	—	—
Familia *Euplotidae* Ehrenberg								
186. *Euplotes balteatus* Dujardin	—	1	2	1	2	2	2	1
187. *E. cristatus* Kahl	—	—	—	—	1	1	—	—
188. *E. elegans* Kahl	—	1	2	—	1	2	2	1
189. *E. elegans* var. *littoralis* Kahl	—	—	1	—	2	1	—	—
190. *E. trisulcatus* Kahl	—	1	—	1	1	1	—	—
191. *E. moebiusi* Kahl	—	2	2	2	2	2	3	1
192. *E. bisulcatus* Kahl	—	1	—	—	1	—	—	—
193. *E. zenkewitchi* Burkovsky	—	—	—	—	—	1	2	—
194. *Discocephalus rotatorius* Ehrenberg	—	1	2	1	2	2	2	1
195. *D. ehrenbergi* Dragesco	—	1	2	1	1	2	1	—
196. *Diophrys scutum* Dujardin	—	2	2	1	2	3	2	1
197. *D. irmgard* Mansfeld	—	1	—	1	1	1	—	—
198. *D. appendiculata* Ehrenberg	1	2	1	1	2	3	2	1
199. *D. histrix* Buddenbrock	2	2	2	2	2	2	2	—
200. *Uronychia transfuga* O. F. M.	1	2	2	2	2	2	2	1
201. *Uronychia* sp.	1	1	1	1	1	1	—	—
Familia *Aspidiscidae* Stein								
202. *Aspidisca steini* var. *major* Budd.	—	2	1	2	3	3	2	1
203. *A. maior* Madsen	—	1	—	—	1	—	—	—
204. *A. psammobiotica* Burkovsky	—	1	—	—	2	3	3	1
205. *A. lyncaster* Stein	—	1	1	—	1	1	—	—
206. *A. sedigita* Quennerstedt	—	2	1	—	—	—	1	—
207. *A. irinae* Burkovsky	—	2	—	1	1	1	—	—
208. *A. dentata* Kahl	—	2	1	1	1	1	—	—
209. *A. fusca* Kahl	—	1	1	1	1	2	1	—
210. *Aspidisca* sp.	—	2	—	—	—	1	1	—

* Детрит, водорослевый ил скопления ничатых водорослей.
** Талломы ламинарий, фукусов, камни, скалы.
*** Для грубой оценки количества инфузорий в пробах применялись следующие обозначения:—инфузорий отсуствуют, 1—инфузорий присуствуют в малом количестве, и не во всех пробах, 2—мало инфузорий, но они присуствуют в пробах постоянно, 3—умеренное количество инфузорий 4—много инфузори, и они встречаются ностоянно.

* Detrite, algial mud, and algial mass.
** Thalli of laminariales and fucaceous algae, surface of stones and cliffs.
*** For rough estimation of the number of ciliates in the samples the following marks were used: complete lack of ciliates, 1 — a small number of ciliates, found not in all samples, 2 — a small number of ciliates, found in each samples, 3 — moderate number of ciliates, 4 — ciliates numerous and found constantly.

По отношению к песчаному биотопу всех инфузорий можно разделить на две большие группы: эврибионтные и стенобионтные виды. Это деление основано на преимущественном распределении инфузорий по биотопам.

К группе эврибионтных видов относятся почти все факультативные мезопоральные и очень многие эврипоральные виды (по классификации Fauré-Fremiet 1950, 1951). Они встречаются в большом количестве помимо песчаного биотопа в скоплениях живых нитчатых водорослей, в детрите, в придонной воде, на поверхности непористого субстрата (глина, скала, слоевища ламинарий и фукоидов), в сильно опреснённых водах (устья ручьёв, заливы, супралиторальные заплески на скалах) и в других биотопах. В предыдущей нашей работе (Бурковский 1967) эти инфузории объединялись под общим названием „эвripоральные инфузории", что не совсем точно. Более удачным определением является термин „эврибионтные инфузории".

Эврибионтные виды населяют все четыре яруса песчаного биотопа (придонную воду, детрит на поверхности песка, поверхность и самый поверхностный слой песчаного грунта и, капиллярные пространства между песчинками, или интерстициаль (Бурковский 1967, 1968 а). Среди инфузорий, обитающих в придонной воде (0–5 см), некоторые являются чисто планктонными животными (*Cyclotrichium sphaericum*, *C. cyclocaryon*, *Askenasia stellaris*, *Didinium balbiani*, *Helicostomella subulata*, *Parafavella denticulata*, *Tintinopsis karajacensis*). Самые мелкие планктонные инфузории встречаются даже глубоко в грунте. Большая часть инфузорий придонной воды относится к факультативным планктонным (*Strombidium* spp. *Mesodinium* spp.) или к бентосным животным (*Prorodon* spp., *Coleps* spp., *Helicostoma* spp., *Ophryoglena marina* и многие другие).

В слое детрита на поверхности песка встречаются самые разные инфузории, причём ведущее место принадлежит тем из них, для которых детрит или развивающаяся на его базе богатая микрофлора, или присутствующие здесь в большом количестве мелкие диатомовые, служат основным источником пищи. Наиболее характерны здесь *Pleuronema coronatum*, *Cyclidium velliferum*, *Cristigera setosa*, *Chlamydodon triquetrus*, *Aspidisca steini* var. *major*, *Frontonia maris-albi*, *Euplotes moebiusi*. Наряду с другими эти же виды были обнаружены в скоплениях нитчатых водорослей и в водорослевом илу.

Поверхность и самый поверхностный слой песка (0–0.5 см) населяют главным образом крупные гипотрихи *Discocephalus rotatorius*, *D. ehrenbergi*, *Diophrys scutum*, *D. irmgard*, *Gastrostyla pulchra*, *Uronychia transfuga* и некоторые другие. Довольно обычными здесь являются также некоторые очень крупные планктонные, факультативные планктонные и бентосные инфузории *Cyclotrichium sphaericum*, *Helicostomella subulata*, *Parafavella denticulata*, *Ophryoglena marina*, *Prorodon moebiusi*. Интересно, что виды *Remanella* в мелкозернистом песке предпочитают также самый поверхностный слой, но в крупнозернистом и среднезернистом песке встречаются только в глубоких слоях грунта. Многие из вышеперечисленных инфузорий были обнаружены на поверхности различных непористых субстратов (талломы ламинарий, камни, скалы), а также в придонной воде.

Эврибионтные инфузории, характеризующиеся мелкими размерами (*Euplotes trisulcatus*, *Euplotes elegans* for. littoralis, *Aspidisca fusca*, *A steini* var. major) или вытянутой формой тела (*Lacrymaria marina*, *Trachelostyla pediculiformis*, *Holosticha diademata*) проникают глубоко в песок и образуют здесь многочисленные популяции. Не менее часто эти инфузории встречаются в других биотопах. Вообще, эврибионтные виды отличаются не только широким и равномерным распределением, но и большей численностью. В этом отношении сравниться с ними могут

немногие интерстициальные инфузории (*Tracheloraphis phoenicopterus, T. incaudatus, Trachelonema oligostriata, Kentrophoros fasciolatus, Remanella margaritifera, R. rugosa, R. granulosa*).

К интерстициальным (стенобионтным) инфузориям следует отнести формы, исключительно или преимущественно населяющие капиллярные пространства в песке. В связи с обитанием в подобных условиях среди них преобладают формы с сильно вытянутым лентовидным или нитевидным телом, высоко сократимые и тигмотактичные формы. Особенно чётко эти приспособления прослеживаются у микропоральных видов (*Tracheloraphis* spp., *Trachelocerca* spp., *Trachelonema* spp., *Helicoprorodon* spp., *Pseudoprorodon* spp., *Remanella* spp., *Geleia* spp., *Kentrophoros* spp., *Blepharisma* spp.) и в значительно меньшей степени у мезопоральных видов (*Loxophyllum* spp., *Coelosomides vermiformis*). Крупнозернистый песок населяют главным образом различные эврибионтные виды. Среди них особое место принадлежит инфузориям с твёрдым панцирем (*Coleps* spp., *Placus* spp., *Plagiopogon loricatus, Leptopharynx torpens*) или другими „скелетными" образованиями (*Aspidisca* spp., *Euplotes* spp.), которые повышают устойчивость животных к механическому повреждению. Это качество особенно важно в прибойной верхней литорали.

Обзор данных по фауне инфузорий морского бентоса

В самые последние годы значительно расширилось наше представление о фауне бентосных инфузорий европейских морей. Наиболее полно изученными следует считать Чёрное и Балтийское моря, а также атлантическое побережье Европы (включая Северное море). В меньшей степени это относится к Средиземному, Белому и Каспийскому морям. Из других более или менее изученных районов мирового океана следует назвать атлантическое побережье Северной Америки. Подобные исследования проводились также в Тихом океане, в Гвинейском заливе и в Антарктике. Однако все они по своей изученности не могут сравниться с европейскими морями.

В настоящей работе были использованы следующие источники: по Каспийскому морю: Агамалиев 1967, по Чёрному морю: Kahl 1930–1935, Валканов 1957, Lepsi 1960, 1962, Tucolesco 1961, 1962 a, Petran 1963, Ковалёва 1966; по Средиземному морю: Kahl 1930–1935, Dragesco 1960, Vacelet 1961 a, 1961 b, Wenzel 1961, Wichterman 1964, Dietz 1964; по атлантическому побережью Европы (включая Северное море): Kahl 1930–1935, Fauré-Fremiet 1950, Dragesco 1960, 1963 a, 1963 b; по Балтийскому морю: Kahl 1930–1935, Воск 1952, 1955, Münch und Petzold, 1955/66, Jaeckel 1962, Biernacka 1962, 1963, Fenchel 1966; по Белому морю: Мережковский 1878, Райков 1962 и собственные данные, изложенные в настоящей работе; по атлантическому побережью Северной Америки: Kahl 1930–1935, Yocom 1930, Lackey 1936, Fauré-Fremiet 1951, Beers 1954, Torch 1961, Borror 1963 a, 1963 b, 1966 a, 1965 b, 1966, Thompson 1964, 1966 a 1966 b; по Гвинейскому заливу — Dragesco 1965; по Японскому морю: Райков 1963. Кроме того в работе учитывались краткие сообщения по фауне различных районов мирового океана: Баренцево море: Гассовский 1916, Райков 1960, Ковалёва 1967; Тихий океан: Ozaki 1941, Thompson 1965 a; Антарктика: Thompson 1965 b и некоторые другие.

В целом для морского бентоса известно свыше 920 видов инфузорий, относящихся к 143 родам (исключаются прикреплённые, симбиотические и паразитиче-

ские формы). Более 20 видов (8 родов) являются планктонными животными, встречающимися однако и в бентосе. Остальные 900 видов (135 родов) исключительно или преимущественно донные формы. По своему происхождению они могут быть разделены на пять групп: 1. инфузории морских родов, 2. инфузории солоноватоводных родов, 3. инфузории смешанных родов, общих для морских, солоноватых и пресных вод, 4. инфузории родов, общих для солоноватых и пресных вод, и 5. инфузории пресноводных родов (Таблица 2).

Таблица 2

Table 2

Характеристика родового состава фауны морей

Characteristic of the generic composition of marine fauna

Роды Genera	Моря Seas								Общее количество Total number	
	C	Bl	M	E	B	W	A	J	роды genera	виды species
Морские Marine	11	17	22	22	16	14	12	13	30	176
Солоноватоводные Brackish water	—	5	2	4	8	—	—	—	9	21
Смешанные (общие для морских, солоноватых и пресных вод) Mixed—common in sea, brackish and fresh waters	33	46	48	54	52	38	35	21	55	595
Общие для солоноватых и пресных вод Common in brackish and fresh water	5	15	8	4	15	5	5	—	25	86
Пресноводные Fresh water	1	8	2	—	1	6	3	—	16	22
Общее коилчество родов Total number of genera	50	91	82	84	92	63	55	34	135	900

Сокращения, принятые в этой и следующих таблицах: C — Каспийское море, Bl — Чёрное море, M — Средиземное море, E — Атлантическое побережье Европы, Eu — все моря Европы, B — Балтиское море, W — Белое море, A — Атлантическое побережье Северной Америки, J — Японское море, G — Гвинейский залив.

Abbreviation used in this and next tables: C — Caspian Sea, Bl — Black Sea, M — Mediterranean, E — European Atlantic, Eu- — all seas of Europe, B — Baltic Sea, W — White Sea, A — North American Atlantic, J — Japan Sea, G — Guinea Gulf.

Инфузории морских родов. Эта группа насчитывает 176 видов (30 родов, относящихся к 17 семействам). Только 4 семейства являются исключительно морскими (*Trachelocercidae*, *Geleidae*, *Coelosomididae*, *Peritromidae*). Богато представленное в море семейство *Loxodidae* также в основном морское. Морские роды, как правило, небольшие и редко включают более 6 видов. К крупным родам относятся роды вышеперечисленных морских семейств (*Trachelocerca* — 21 вид, *Tracheloraphis* — 35 видов, *Trachelonema* — 8 видов, *Remanella* — 17 видов, *Kentrophoros* — 11 видов, *Geleia* — 16 видов, *Peritromus* — 7 видов). Большая часть морских родов в своём составе имеет 1–3 вида. Сравнительная

немногочисленность морских родов и их малый состав частично объясняются недостаточной изученностью морских инфузорий.

В экологическом отношении инфузории морских родов исключительно однородная группа. Подавляющее большинство инфузорий — интерстициальные животные.

Инфузории солоноватоводных родов. К этой группе относится 21 вид (9 родов). Причём на долю двух таких родов, как *Sonderia* и *Protocrucia*, известных для Чёрного, Средиземного, Северного и Балтийского морей, приходится 13 видов. Остальные 7 родов содержат по одному виду и являются эндемиками.

Почти все инфузории этой группы — псаммофильные животные.

Инфузории смешанных родов. Подавляющее большинство видов бентосных инфузорий, встречающихся в морских и солоноватых бассейнах относятся к смешанным родам (595 видов, 55 родов). Смешанные роды очень крупные и включают до нескольких десятков видов. Они входят в состав большинства отрядов и характеризуются очень разнообразной морфологией.

В экологическом отношении инфузории этих родов чрезвычайно разнообразны. Они населяют самые различные биотопы в море, в солоноватых и пресных водах и в большинстве являются эврибионтными видами. Однако среди инфузорий немало и таких, которые населяют исключительно или преимущественно капиллярные пространства в песке (*Blepharisma clarissimum*, *Condylostoma remanei*, *Keronopsis rubra*, *Pseudeprorodon arenicola*, *P. mononucleata*, *Loxophyllum vermiforme* и другие).

Инфузории родов, общих для солоноватых и пресных вод. Обычно они свойственны пресным и слабо солоноватым водоёмам, но встречаются также и в морских водах. Главные роды: *Metopus*, *Spirostomum*, *Parablepharisma*, *Uroleptus*, *Paramecium*, *Stentor*. К этой группе относится 86 видов инфузории (25 родов).

Инфузории пресноводных родов. Они характерны только для пресных вод. Проникновение этих инфузории в солоноватые и морские воды следует считать случайным. Однако присутствие в водоёме инфузории этой и предыдущей групп специфически определяет его фауну. В общей сложности в полигалинных водоёмах встречаются 22 вида пресноводных инфузории (16 родов).

Географическое распространение морских бентосных инфузорий

Сравнительные данные по фауне различных морей и районов представлены на Таблице 3. В верхней правой половине таблицы сравнивается родовой состав фаун водоёмов, в нижней левой-видовой состав. Причём, в числителе показано абсолютное количество видов (или родов), общих для двух сравниваемых водоёмов, в знаменателе — его процентное выражение к общему числу видов (или родов), известных для обоих районов. Процент общих видов (или родов) вычислялся по формуле: $\frac{C}{A+B-C}\ 100\%$, где A количество видов (или родов), известное для одного района, B — для другого района, C — число видов, общих для двух районов. По диагонали даны абсолютные значения родов (в числителе) и видов (в знаменателе), известные для каждого отдельного водоёма.

Нетрудно заметить, что самые высокие проценты общих видов (и родов) свойственны хорошо изученным и смежным европейским водоёмам. Однако

Таблица 3
Table 3
Сравнительные данные по фауне морских водоёмов*
Comparison of marine faunas

	C	Bl	M	E	B	W	A	J
C	50 / 119	41 / 40.1%	39 / 42%	38 / 40.8%	45 / 46.3%	41 / 57%	35 / 50%	26 / 45%
Bl	57 / 16.7%	91 / 300	64 / 58.7%	63 / 58%	68 / 54%	51 / 49.5%	49 / 50.5%	30 / 35.8%
M	45 / 17.6%	78 / 19.3%	82 / 181	64 / 62.7%	65 / 60.6%	47 / 49.8%	45 / 48.9%	32 / 38%
E	58 / 16.6%	103 / 21.2%	79 / 20.3%	84 / 288	68 / 63%	53 / 56.1%	45 / 47.8%	34 / 37%
B	69 / 19.9%	120 / 24.7%	83 / 20.6%	112 / 23.3%	92 / 305	52 / 52%	46 / 45.5%	33 / 34%
W	51 / 18.9%	93 / 22.7%	63 / 19.7%	100 / 25.6%	108 / 27%	63 / 202	40 / 51%	31 / 47%
A	30 / 12.5%	64 / 16.5%	47 / 18.4%	50 / 12.8%	70 / 18%	60 / 20.3%	55 / 153	26 / 41%
J	35 / 23.3%	35 / 10.6%	33 / 15.4%	41 / 13.1%	43 / 13.4%	45 / 20%	29 / 14.2%	34 / 66

* Объяснение в тексте.

* In the upper right part of Table 3 there are compared the generic composition of the marine fauna, in the lower left part the specific composition. The numerator gives the absolute number of species (or genera), which are common in two compared seas, the denominator gives its percentage as compared with the whole number of species (or genera), which are known in both seas. The absolute number (genera in the numerator and species in the denominator), known for each sea or region, are given on the diagonal.

в среднем они не превышают 25% для видов и 60% для родов. Проценты общности для менее изученных европейских морей несколько ниже, но в целом остаются близкими к 20% (исключение составляет Каспий, у которого он равен 18%). Вместе с тем нельзя не обратить внимания на то, что процент общности остаётся почти неизменным в пределах Европы и в очень малой степени зависит от удалённости сравниваемых водоёмов. Это свидетельствует с одной стороны о целостности фауны Европы, с другой — о том, что основной объём общих видов составляют одни и те же широкораспространённые формы.

Действительно, число видов, свойственных трём и более бассейнам равно 179, что составляет 19.9% от общего числа видов, известных для морского бентоса (Таблица 4). Среди них около половины видов характеризуются прерывистым ареалом, что позволяет надеяться на нахождение, возможно, многих из них в промежуточных водоёмах, и на некоторое повышение за счёт этого процента общих видов. Не исключено и обратное — некоторые виды, с большим разрывом в ареале могут оказаться разными видами.

Оставляя в стороне спорные вопросы, перейдём к рассмотрению зависимости количества видов, общих для двух и более бассейнов, от числа сопостав-

Таблица 4

Table 4

Количество видов, общих для разного числа морей

Number of species common to different numbers of seas

Количество морей Sea number	2	3	4	5	6	7	8	9	Всего Total
Количество видов Number of species	519	179	114	73	49	33	18	5	519
Процент от общего количества видов (900) Per cent from total number of species	57.8	19.9	12.6	8	5.4	3.6	1.9	0.5	57.7

ляемых бассейнов. Как показывают данные Таблицы 4, она обратная. Чем больше рассматриваемый нами район, тем меньше видов, общих для разных его частей. Можно все же предположить, что в будущем количество видов, общих для этих районов существенно возрастёт. Однако, маловероятно, что это существенно отразится на соотношении общих видов ко всему количеству видов в бентосе мирового океана. Надо полагать, что в дальнейшем будут не только переоткрываться известные виды, но и описываться новые (особенно в мало или совсем неизученных районах мирового океана).

В Таблицах 5–6 приведены данные о видах, общих для двух или трёх, или четырёх районов, географически удалённых друг от друга (Европа, Атлантическое побережье Северной Америки, Японское море и Гвинейский залив). Наибольшее количество общих видов свойственно Европе и Америке, наименьшее — Гвинейскому заливу и Японскому морю, что хорошо согласуется с общепринятым мнением в отношении других групп морских животных. Виды, общие для трёх любых географически отдалённых районов, составляют в среднем 1.5%, а всех четырёх — 1% от общего количества инфузорий, известных для морского бен-

Таблица 5

Table 5

Количество видов, общих для двух географически отдаленных районов

Number of species common to two geographically remote areas

Районы Areas	Eu-A	Eu-J	Eu-G	A-J	A-G	G-J
Количество видов Number of species	104	62	45	29	27	19
Процент от общего количества видов (900) Per cent from total number of species (900)	11.6	7	5	3.2	3.1	2.1

Таблица 6

Table 6

Количество видов, общих для трёх и четырёх географически отдалённых районов

Number of species common to 3 and 4 geographically remote areas

Районы Areas	Eu-A-J	Eu-G-Ja	Eu-G-A	A-J-G	Eu-A-J-G
Количество видов Number of species	16	15	12	10	9
Процент от общего числа видов (900) Percentage expression (total 900 species)	1.7	1.6	1.3	1.1	1

Таблица 7

Table 7

Анализ видового состава инфузорий различных морей

Analysis of ciliate species composition of different seas

Моря Seas		C	Bl	M	E	B	W	A	J	Всего Total
Эндемичные виды Endemic species	количество number	14	73	48	76	71	20	49	6	381
	удельный вес в % per cent of fauna	11.8	24.3	26	26	23	10	32	9	
Виды свойственные 2 районам Species characteristic for 2 areas	количество number	26	109	52	94	104	84	34	12	340
	удельный вес в % per cent of fauna	22.6	33.3	29	32.5	32.6	21.7	18	20	
Виды свойственные 3 и более районам Species characteristic for 3 and more areas	количество number	79	118	81	118	130	101	70	48	179
	удельный вес в % per cent of fauna	65.6	39.4	45	41.5	42.5	50	46.3	73	
Общее количество видов Total number of species		119	300	181	288	305	202	153	66	900

тоса. Эти проценты слишком малы, чтобы подтвердить гипотезу космолитного распространения морских инфузорий.

В экологическом отношении широко распространённые инфузории — эврибионтные виды, но 40 видов-интерстициальные инфузории. Именно поэтому в морском песке удельный вес широко распространённых форм выше, чем в любом другом морском биотопе.

По имеющимся в настоящее время данным, удельный вес широко распространённых видов (свойственных трём и более бассейнам) в хорошо изученных европейских морях не превышает 43% (Таблица 7). Благодаря их высокой численности в морском бентосе они обнаруживаются в первую очередь, а при поверхностном изучении водоёма, они преобладают в списке фауны. Сравнение таких поверхностно изученных районов даёт неверное представление о большой степени общности их фаун. При достаточно полном изучении фауны моря выясняется, что более 55% видов приходится на долю инфузорий, свойственных только одному или двум морям. Причём по отношению к общему количеству видов, известному для морского бентоса, они составляют более 80%. Особенно высоким оказывается число эндемичных видов. Конечно, быть может, многие из них в дальнейшем будут обнаружены в соседних водоёмах, а некоторые являются продуктом ошибочного определения. И всё же, даже учитывая это, необходимо отметить, что такое высокое содержание эндемичных видов в морских водоёмах — явление исключительное и трудно объяснимое с точки зрения космополитного распределения инфузорий.

В заключение следует отметить, что имеющиеся в настоящее время данные не позволяют прийти к сколь-нибудь определённому мнению о географическом распространении морских бентосных инфузорий. Возможно, что инфузории занимают особое место в зоогеографии. Пока неизученными остаются огромнейшие пространства мирового океана, ко всякого рода обобщениям в области географического распространения морских инфузорий следует пдходить с большой осторожностью.

Резюме

В работе приводятся сведения по фауне и экологии бентосных инфузорий Белого моря, анализируется родовой и видовой состав инфузорий различных морских водоёмов, а также обсуждается вопрос о географическом распространении морских бентосных инфузорий.

Summary

In the present paper information are given about fauna and ecology of benthic ciliates of the White Sea together with an analysis of the generic and specific composition of benthic ciliate fauna in other seas and discussion on their geographical distribution.

The author found 210 species of ciliates in sands of the White Sea; 135 of them were found for the first time in the White Sea and 17 were new. Descriptions of these new species are given in the former author's papers. In general the fauna of benthic ciliates of the White Sea has marine character, but 15% of it brackish- and fresh-water species. About one half of the fauna consists of eurybiontic ciliates, the rest are interstitial species (Table 1). The eurybiontic species inhabit all the

four layers of the sand biotop (the layer of water at the bottom, detrite, sand surface, superficial layer of sand, and the capillaries between the sand grains, or interstitial), the interstitial species occur mainly in the capillaries between the sand grains.

In the World Ocean about 900 species of benthic ciliates are known (except of symbiotic, sedentary or parasitic forms). According to their origin they may be divided into 5 groups: 1 — ciliates of marine genera, 2 — ciliates of brackish water genera, 3 — ciliates of mixed genera occurring in salt-brackish- and fresh-water, 4 — ciliates of mixed genera occurring in brackish- and fresh-water, 5 — ciliates of fresh water genera (Table 2). These groups differ by their ecology. Marine and brackish water ciliates are usually interstitial organisms, the ciliates of mixed genera are eurybiontic ones. The fact that the group of marine ciliates is not numerous and most of the genera contain only 1–3 species may be partly explained by little information we have about them. Fresh water ciliates and the ciliates commonly occurring in fresh and brackish water are accidental ones in the sea sand but they characterize specifically the fauna of given sea.

While discussing the question of geographical distribution of the marine benthic ciliates (see Tables 3–7) the author makes a conclusion that all up to date known facts completely contradict the hypothesis of cosmopolitic distribution of marine ciliates. The main argument against this hypothesis is the existence of a great number of endemic and little distributed species which constituted more than 80% of all known species. In the author's opinion the generalization on the geographical distribution of marine benthic ciliates must be taken with great carefulness as the vast spaces of the World Ocean have not been yet investigated.

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The influence of formalin on morphogenesis of *Chilodonella cucullulus* O. F. Müller

Wpływ formaliny na morfogenezę *Chilodonella cucullulus* O. F. Müller

The action of formalin on morphogenesis and division of ciliates was investigated by Fauré-Frémiet 1944, 1945, 1948, Corliss 1953 a, Suzuki 1960, Puytorac et Paret 1965. It follows from their studies that this agent exerts a multidirectional action upon the above processes.

The observations of Suzuki 1960 indicate a resorption of newly arising structures and inhibition of macronucleus division. They reveal also a different degree of susceptibility to formalin of different development stages of *Blepharisma undulans*.

Puytorac et Paret 1965 observed that after the application of formalin to the trophotomonts of *Ophryoglena*, different degrees of degradation of cortical structures occur in tomits, as well as disturbances of their division.

Fauré-Frémiet 1944, 1945, 1948 and Corliss 1953 suggest the possibility of inhibition of cytokinesis itself by formalin. In the case of irreversible disturbances in division, the action of formalin leads to formation of persisting or transistory chain doublets, the latter ones only then if the impairment has been repaired. This factor may possibly act upon the cytokinetic spindle in a reversible manner like the "freezing" substance (Mazia and Zimmermann 1958).

Observation of susceptibility to formalin in the individuals of *Chilodonella cucullulus* of the same age, at different development stages permitted to determine the action of this agent upon morphogenesis and division. The disturbances evoked by formalin in developmental processes enabled to establish the degree of association of separate morphogenetic processes providing simultaneously a possibility of an attempt of experimental distinction of stomatogenesis, morphogenesis of CVP, macronucleus division and cytokinesis.

The preliminary studies indicated that low concentrations of formalin are not highly toxic i.e. the moment of ciliate death may be delimited from the moment of manifestation of disturbances in developmental processes when however the capability of performing the fundamental life functions has been preserved. The external effect of formalin action in the form of changes in the activity of cilia, are manifested earlier than the changes of intracellular structure. This indicates a considerable degree of impermeability of the superficial layers in *Chilodonella cucullulus*.

Material and methods

For the study, a population of *Chilodonella cucullulus* was used cultivated in the Zoology Institute, Protozoological Laboratory, Warsaw University. The cultures isolated from the culture B_1 (Kaczanowska and Kowalska 1969) were kept in Petri dishes in an undefined medium. Ciliates were inoculated every day into tap water and fed with suspension of fresh yeast. The temperature in which cultures were kept fluctuated from 18°C to 23°C. Light microscope with phase contrast was used. Preparations were executed by Chatton–Lwoff method modified by Corliss 1953 b. Pure pro analysis farmalin neutralized with $CaCo_3$ was used. Different concentrations were prepared with tap water. For each series of experiments freshly prepared solutions were applied.

Results

One of the preliminary problems was the determination of the lethality curve at the range of formalin concentration from 10^{-2} to 10^{-3}% (Fig. 1). The

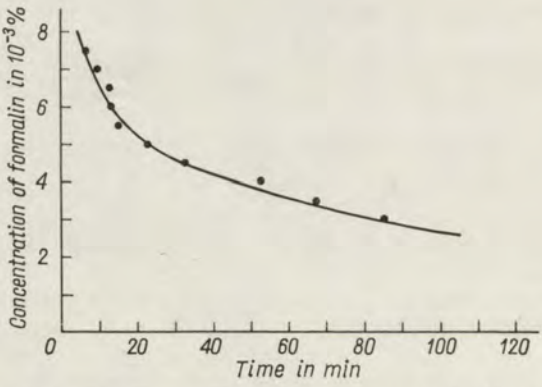

Fig. 1. Longevity of *Chilodonella cucullulus* in low concentration of formalin. Points represent the moment of death of 80 per cent of individuals

number of individuals in one sample amounted about 60. The moment of nearly simultaneous death of 80% of individuals was accepted as the lethal time. The criterion of 80% instead of 50% was applied considering the possibility of a considerable dispersion of survival of individuals which are in the same stage of cell cycle as reported by Suzuki 1960 for *Blepharisma undulans* when treated with constant concentrations of formalin for the same period of time. In this way the time of action of formalin concentrations from 8.10^{-3}–3.10^{-3}% was determined and applied in the experiments.

Manner of formalin penetration

For revealing the manner of formalin penetration into the cell of *Chilodonella cucullulus*, the plasmal reaction was applied consisting in staining with the Schiff reagent the aldehyde groups liberated by formalin in cytoplasm. 20% formalin was used. In effect, the area of basket and the cytoplasm stripe

from mouth to the body inside were most intensely stained. Formalin penetrates distinctly per os.

The control material fixed with the Carnoy reagent was treated with formalin, rinsed and stained with Schiff's fuchsine. Macronucleus and cytoplasm became uniformly light red. In this case formalin penetrated distinctly across the entire body surface.

The experiments were supplemented by the study of survival in $7.10^{-3}\%$ formalin of conjugant-ciliates with non-functioning mouth. It was found that some conjugants survive longer (approx. 20 min) than non-conjugants.

Effect of low formalin concentrations on trophic individuals of *Chilodonella cucullulus*

In the initial period of the study, $2.5 \cdot 10^{-3}\%$ formalin concentration was applied for about 2 hours. It was presumed that after such a long action of formalin, at least some ciliates might be in the ontogenesis stage of a maximal susceptibility and would manifest inhibition of development processes either as anomalies or as arrest at a most susceptible stage of ontogenesis. Indeed, among the ciliates studied appeared a few — when compared with the control sample — dividers. Those ciliates were at different stages of development after having been placed two hours later into fresh water. Such a behaviour of ciliates is possibly a result of slowing or of inhibition of — at least — some of the metabolic functions and of a fall of division rate and not of blockage of one definite stage.

Subsequently the action of $6.5 \cdot 10^{-3}\%$ formalin was experimented. It kills ciliates within 10–12 min. Dense samples of ciliates sampled at random were treated with this formalin concentration in sublethal time. Formalin acts in the first place on the motor apparatus. Ciliates gradually slow their movement. After a prolonged action of formalin, ciliates lost their capability of motion and perished. When transferred into water at the sublethal time, ciliates normalize all their life functions within several minutes, they regain movement, food uptake, action of CVP and defecation.

Further observations showed that ciliates approach cytokinesis with delay. They either divide fully or undergo an uncomplete division remaining in the form of doublets for a more or less prolonged time. Fixation at the second and sixth hour after the treatment with formalin revealed the presence of dividers. Possibly those dividers were a slow continuation of processes which had begun prior to the action of formalin or occurred after the period of repairing the damage. Those possibilities have not been followed.

Action of formalin on *Chilodonella cucullulus* individuals at the stage of early cytokinesis

Formalin of $7.8 \cdot 10^{-3}\%$ concentration was applied to dividers for 4 min. All the ciliates accomplished their cytokinesis without disturbances. Results which would support the observations of Fauré-Frémiet 1948 on *Didinium nasutum*, have never been obtained.

In another series of experiments, a $6.5 \cdot 10\%$ concentration has been used for the sublethal time of 10 min. Dividing ciliates were treated with formalin, isolated subsequently into tap water and rinsed several times. All the individuals concluded their cytokinesis without delay. However in some individuals of their second generation an uncomplete division was observed. Among 130

individuals studied, 18 doublets were found (nearly 14%), however the observations were carried out for less than 24 hr and some new doublets could possibly arise.

All the doublets obtained in the second generation were asymmetric, the deviation running along the anterio-posterior axis. They were not stable and separated proportionally to the degree of advancement of cytokinesis. According to Tartar 1961, the stability of doublets depends on its symmetry. In my experiments, doublets were asymmetric and unstable.

It occurred in four doublets out of 18 that at an uncomplete cytokinesis only one component had macronucleus. In this case, after the fission of doublets one component was deprived of macronucleus and perished soon, the other one produced normal individuals after its division.

The fission of doublets had not a character of accomplishment of the interrupted cytokinesis but rather of a mechanical separation, similarly as it was observed by Dawson 1920 in *Oxytricha* and by Totwen-Nowakowska 1964 in *Stylonychia mytilus*. The separated components produced a population of single normal individuals.

Action of formalin on individuals of *Chilodonella cucullulus* in the same stage of the cell cycle

Susceptibility of ciliates to formalin has been observed at different stages of their ontogenesis (Table 1). Individuals in the same age were treated with $6.5 \cdot 10^{-3}$ % formalin for 10 min. Subsequently ciliates were isolated on slides with concavities rinsed with water and left in humid chamber. The individuals which failed to renormalize their movement even after repeated rinsing were eliminated from the experiment.

The mean time of generation of the control samples fluctuated within the range of 11–13 hr. The study revealed that the maximal susceptibility is that of the 8-hours ciliates. The retardation of division amounts then 4–8 times of generation time. In this series, 4 doubles were observed. The minimal susceptibility is that of 11-hr individuals. In most cases their ontogenesis is prolonged only by one generation time. Among the 6-hr ciliates only 2 doublets were observed (Table 1).

Doublets obtained in the first generation were identical with the doublets evoked in the second generation i.e. are asymmetric and unstable. Two doub-

Table 1

Effect of formalin on individuals of *Chilodonella cucullulus* in different stages of the life cycle

Age of individuals (hours after division)	Retardation of division (in hours)								Number of tested individuals
	12	24	36	48	60	72	84	96	
2			24						24
4		1	34						35
6				41	6				47
8		3		12	12	8		11	46
9			1	12	7				20
10	5	23	9	8					45
11	15	11	4						30

lets produced monstra as results of uncompleted divisions. Monstra failed to take food and perished after several days without either dividing or separating.

Growth of ciliates and their behaviour after the action of formalin

Doublets of the chain type were not obtained either in the first or second generation. The ciliate division was disturbed but proter and opistor grew and changed their mutual position. Finally they became joined by their dorsal surfaces. Doublets of a similar type were obtained by MacDougall 1929 by the action of UV-rays upon *Chilodonella uncinatus*.

Among the individuals retarded in their division for several generations the cases of gigantism were not observed although they normally took food. They preserved their normal movement and their food vacuoles functioned without disturbances.

Discussion

The degree of susceptibility to formalin expressed in prolongation of the generation time, rises with the age of the individual of *Chilodonella cucullulus*.

The eighth hour of the life cycle may be accepted as the critical moment within the 11–13 hours-long ontogenesis of the ciliate. At this stage of development considerable differences of susceptibility to formalin appear. Possibly this factors is impairing the processes which initiate cytogenesis. Repairing of those damages requires a multiple time of generation.

The 11-hours individuals i.e. those which enter the division phase, have after the action of formalin a prolonged ontogenesis, mostly for a time of one generation. This may be explained by the fall of susceptibility in the structures associated with the cytokinesis of the first generation.

When treated with formalin, the dividing individuals accomplish their division with no dalay and disturbances. However the doublets occurring in cytokinesis of the second generation indicate that formalin acts upon the preparation phase to division or upon the mechanism controlling this preparation. Perhaps this agent acts upon the dividing ciliates in a similar way as CO_2 does upon the egg of echinoderms being at the last stage of cytokinesis (Mazia 1961).

The similarity of doublets evoked in the first and second generations suggests a similar nature of impairments evoked by formalin.

After the action of formalin, a regular cortical morphogenesis was always observed. However in many cases a full cytokinesis failed to occur, in some of them macronucleus did not divide either. Consequently the doublets evoked by formalin present an example of experimental separation of morphogenetic processes.

The results of the present study indicate however a multidirectional action of formalin and this fact accounts for the divergence of effects gained on different objects by the authors.

Summary

The influence of formalin upon the individuals of *Chilodonella cucullulus* of different stages of life cycle was studied. Formalin proved to penetrate mostly per os.

The stage most susceptible to formalin was found the eight hour of development within the 11–13-th hour long period of ontogenesis. The susceptibility falls down when the cilliate approaches to the cell division. Dividing individuals treated with formalin accomplish their division with no delay or disturbances. Observations of the second generation of those individuals permitted to reveal the non-accomplished division in some of them. As a result, the asymmetric and unstable doublets were formed. In several cases the incomplete cytokinesis was accompanied by the absence of the macronucleus fission.

STRESZCZENIE

Badano wpływ formaliny na różnowiekowe osobniki *Chilodonella cucullulus*. Okazało się, że formalina głównie penetruje per os.

Najwrażliwszym na formalinę stadium przy 11–13 godzinnej ontogenezie orzęska jest stadium w ósmej godzinie rozwoju. Wrażliwość ta maleje wraz ze zbliżaniem się zwierząt do podziału. Traktowane formaliną osobniki dzielące się kończą podział bez zakłóceń i opóźnień. Obserwacja drugiego pokolenia tych osobników pozwoliła wykryć niedokańczanie podziału przez niektóre z nich. W wyniku tego powstawały asymetryczne i nietrwałe dublety. W kilku przypadkach niecałkowitej cytokinezie towarzyszył brak podziału makronukleusa.

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Паразитические инфузории *(Urceolariidae, Peritricha)* прудовых рыб

The parasitic ciliates (*Urceolariidae, Peritricha*) of pond fishes

Паразитические инфузории семейства *Urceolariidae* широко распростанены в различных водоемах СССР как среди морских, так и пресноводных рыб. Изучению этой группы паразитов посвящено большое число отечественных и зарубежных работ однако, большая часть их касаются вопросов морфологии и систематики; данные по биологии триходин, в частности прудовых рыб, немногочисленны. Изучение биологии различных представителей этого семейства представляет не только теоретический, но и практический интерес. Интенсивные формы ведения прудового рыбоводства предусматривают выращивание рыбы при уплотнённых посадках, что способствует тесным контактам, а следовательно, распространению паразитов с прямым циклом развития, в том числе и паразитических инфузорий.

В конце пятидесятых годов в прудовые хозяйства страны из реки Амур и Китая были завезены растительноядные рыбы: белый амур, обыкновенный и пёстрый толстолобики, которые подвержены заражению триходинами в большей степени, нежели карп (Chen Chih-leu 1955, 1956). Совместное выращивание этих рыб также способствует накоплению паразитов в прудах.

Многие авторы, указывая на заражение рыб триходинами, не проводили определения их до вида и только в самое последнее время появились работы, в которых приводятся данные о заражении растительноядных рыб и карпа (Османов 1964, 1965; Слухай 1966; Чернова 1964; Уразбаев 1967; Диарова 1967; Ивсик 1957, 1966; Иванова 1966, 1967; Kazubski and Migala 1968). различными представителями семейства *Urceolariidae* с определением видовой принадлежности паразитов.

В задачу наших исследований входило: выяснение видового состава триходин прудовых рыб, их распространение в рыбоводных хозяйствах центральных и южных районов РСФСР, а также изучение некоторых вопросов биологии основных представителей.

Сбор материала проводился в период с 1964 по 1967 годы. За это время обследовано 2100 экземпляров рыб от личинки до производителей, относящихся к 4 видам: карп (*Cyprinus carpio* L.), белый амур (*Ctenopharyngodon idella* Valenciennes), белый толстолобик (*Hypophthalmichthis molitrix* Valenciennes), пёстрый толстолобик (*Aristichthys nobilis* Richardson) в Московской области:

рыбплемхоз Якоть и Загорский (близ городов Дмитров и Загорск) и Краснодарском крае: рыбопитомник Горячий ключ, рыбхозы Читук и Шапсугский (около города Краснодара) и рыбхоз Синюхинский, расположенный недалеко от города Курганинска.

Определяли видовую принадлежность триходин на мазках в соскобах с поверхности тела и жабр, одну часть которых импрегнировали 2% раствором азотнокислого серебра по методу Клейна, другую фиксировали жидкостью Шаудина для дальнейшей окраски гематоксилином. Среднюю интенсивность инвазии подсчитывали из 25 полей зрения микроскопа при увеличени 7×9×1.6. Все приведенные в работе цифры интенсивности инвазии выражают средное количество паразитов в одном поле зрения. Изготовлено более 600 постоянных препаратов, которые хранятся в коллекции лаборатории.

Контроль за интенсивностью и экстенсивностью заражения проводили круглый год. Летом наблюдения проводили в нерестовых выростных и нагульных прудах. В зимний период исследуемые виды рыб содержали в специальных сетчатых садках, установленных в зимовальных прудах. В трё садках рыбы находились изолированно по видам, в четвёртом все три вида рыб вместе.

Установлено, что в прудовых хозяйствах средней полосы и юга РСФСР паразитируют, в основном, 6 видов кругоресничных инфузорий, относящихся к 4 родам: *Trichodina domerguei* f. *acuta* Lom, 1961, *T. pediculus* Ehrenberg, 1838, *T. mutabilis* Kazubski et Migala, 1968, *T. nigra* Lom, 1960, *Trichodinella epizootica* (Raabe, 1950), *Tripartiella bulbosa* (Davis, 1947).

В разные сезоны года паразитируют различные виды триходин (Рис. 1). *T. domerguei* f. *acuta* встречается в течение всего года на карпе и в небольших

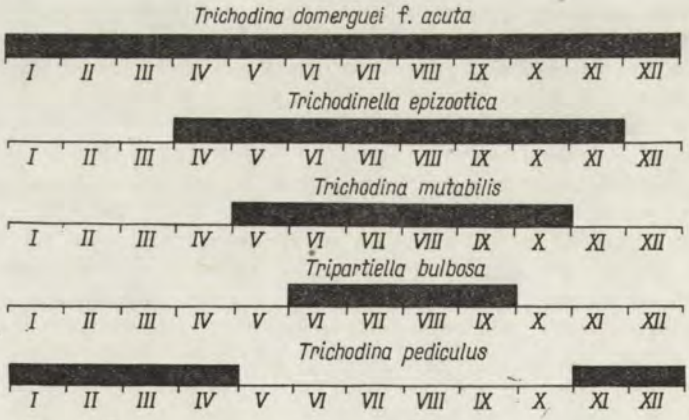

Рис. 1. Распространение *Urceolariidae* по сезонам года
Fig. 1. The distribution of *Urceolariidae* in the seasons of the year

количествах на растительноядных рыбах. Локализуется паразит чаще на коже и реже на жабрах. Заражение мальков карпа происходит на 4–5 день после выклева из икры. В возрасте 20–26 дней заражённость составляет от 1 до 150 паразитов. Интенсивность инвазии сеголетков в течение последующих месяцев незначительная и составляет 0.2–0.3. Для годовиков наибольшее заражение наблюдается в конце зимовки: в марте–апреле при средней интенсивности инвазии 0.9–1.8. Рыбы старших возрастов и производители заражены значительно слабее при средней интенсивности инвазии 0.1. Первые делящиеся формы этого

вида встречаются уже в феврале при температуре воды 0.5–0.7°. В последующие месяцы число делящихся форм увеличивается, достигая максимума в марте–апреле при температуре вода 1–5°.

T. pediculus встречается зимой и ранней весной. Локализуется на коже и редко на жабрах. Так, максимальная заражённость кожи белого амура составила 3.0, а жабр 0.04. Впервые этот вид обнаружен нами на растительноядных рыбах и карпе из зимовальных прудов рыбплемхоза Якоть, Московской области. Единичные экземпляры его появляются уже в январе, а в феврале встречаются делящиеся формы. Наибольшая интенсивность инвазии отмечается в марте–апреле и составляет для белого амура 3.0, белого толстолобика 2.9, карпа 1.0–1.8. В летний период паразит ни разу не был обнаружен.

Следует отметить, что при совместном содержании растительноядных рыб и карпа *T. domerguei* f. *acuta* встречается на первых крайне редко. Что касается *T. pediculus*, то нашими трёхлетними наблюдениями установлен интересный факт нарастания численности этого паразита в зимовальных прудах рыбплемхоза Якоть и постепенного вытеснения *T. domerguei* f. *acuta*, который ранее был основным видом для карпа. Так, в 1964 году *T. pediculus* встречался в основном у белого амура, белого и пёстрого толстолобиков и лишь в небольших количествах был найден у карпа. В 1965 году карп оказался поражён *T. pediculus* в большей степени, нежели *T. domerguei* f. *acuta* не только при совместном содержании с растительноядными рыбами, но и при изолированном, а в 1966 году паразит стал доминирующим у карпа, в то время как *T. domerguei* f. *acuta*, преобладающий у него ранее, встречался теперь в единичных экземплярах. Наши данные вполне согласуются с данными Штейн (1967), которая в числе малоспецифичных форм триходин указывает *T. pediculus*.

T. pediculus как и *T. domerguei* f. *acuta* встречается вместе с *Chilodonella cyprini, Ichthyophthirius multifiliis* и различными представителями рода *Apiosoma*.

В конце апреля — начале мая на карпе, белом амуре, белом и пёстром толстолобиках появляется *Trichodinella epizootica*, встречающаяся до октября. На прудовых рыбах этот вид найден Османовым с соавторами (1966), Диаровой (1967). Локализуется паразит только на жабрах. Единичные особи появляются в конце апреля — начале мая при температуре воды 4–5°. В мае при повышении температуры воды до 15–17° интенсивность инвазии увеличивается. В конце мая — начале июня мальки в возрасте 20–26 дней заражены *T. epizootica* на 90% при средней интенсивности инвазии 0.2–0.3. Интересно отметить тот факт, что в это время *T. epizootica* отмечена на коже мальков, когда процент заражения составил 25, а интенсивность инвазии 0.4. Очевидно, этот факт можно объяснить недостаточными размерами в это время жаберных лепестков для прикрепления на них *T. epizootica*, а следовательно такой небольшой интенсивностью их на жабрах. Годовики в мае заражены значительнее при средней интенсивности инвазии на жабрах 3.3. Высокие летние температуры угнетают паразита. В июле–августе при температуре воды 22–23° интенсивность инвазии резко снижается, составив 0.6. К осени интенсивность инвазии снова увеличивается, составляя для сеголетков 3.1–3.4, а для двухлетков — 0.1–0.7. Встречается *T. epizootica* как в чистом виде, так и в смешанной инвазии с другими представителями семейства *Urceolariidae*, а также с моногенетическими сосальщиками рода *Dactylogyrus*.

T. mutabilis и *T. nigra* паразитируют совместно на карпе, белом амуре, белом и пёстром толстолобиках. Локализуются паразиты чаще на концах респираторных складочек жабр и лишь в небольших количествах встречаются на коже.

На карпе *T. nigra* найден Диаровой (1967) в прудовых хозяйствах Казахстана, а на белом амуре Черновой (1964) в прудовых хозяйствах Грузии. Следует отметить, что из двух видов в нашем материале численно преобладали *T. mutabilis*.

Единичные экземпляры *T. mutabilis* появляются в мае при температуре 15–17°. У сеголетков карпа интенсивность инвазии на концах респираторных складочек составляет 2.7, а на коже — 0.6; у двухлетков соответственно 0.7 и 0.2. Наибольшее заражение наблюдается в июле–августе при температуре воды 20–21°. В это время происходит интенсивное размножение обоих видов, когда встречаются многочисленные делящиеся формы. Позднее со снижением температуры воды до 12–13° интенсивность инвазии сеголетков снижается до 0.08–0.1.

T. bulbosa, найденная нами впервые в Краснодарском крае, позднее была обнаружена на белом амуре, белом и пёстром толстолобиках в хозяйствах, расположенных под Москвой и Рязанью, куда были завезены растительноядные рыбы. Локализуется паразит только на жабрах. На юго он появляется весной, а наибольшая интенсивность инвазии наблюдается в летний период. В средней полосе *T. bulbosa* начинает встречаться позже, в июле–августе, в это время отмечается и наибольшее заражение. Так, зараженность белого толстолобика составляла 30% при интенсивности инвазии 5.6. Пёстрый толстолобик заражён на 90–100% при интенсивности инвазии от 1.9 до 6.4. На юге пёстрый толстолобик заражён на 70–100% при довольно высокой интенсивности инвазии, составляющей 4–30. Белый амур и белый толстолобик заражены в меньшей степени, что отмечено и для средней полосы. На карпе за весь период проведения работ этот вид встречен один раз в единичных экземплярах, поэтому мы считаем возможным предположить, что *T. bulbosa* специфичен к рыбам сино-индийского фаунистического комплекса.

Интересно отметить, что рыбы старших возрастов заражены значительно слабее или совсем не заражены различными видами триходин. Так, в средней полосе интенсивность инвазии для пёстрого толстолобика составила 3.1, а трёхлетков — 0.2. На юге старшие возраста рыб почти совсем свободны от этих паразитов.

Жаберные формы триходин, также как и паразитирующие на коже, встречаются чаще в смешанной инвазии друг с другом и в паразитоценозе с *Myxobolus pavlovskii*, представителями рода *Apiosoma* и моногенетическими сосальщиками рода *Dactylogyrus*. С последними они, вероятно, находятся в антагонистических отношениях. Из 100 случаев у 15% рыб при наличии на жабрах моногеней триходин не отмечено совсем. На зависимость жаберных видов триходин от наличия моногенетических сосальщиков указывают Ивасик (1957, 1966), Sassman (1966).

Изучение патогенной роли различных видов семейства *Urceolariidae* проведено на гистологических препаратах. В статье мы приводим данные о влиянии двух видов на ткани хозяина: *T. mutabilis* и *T. epizootica*. Кусочки жабр фиксировали 4% формалином, заливку проводили в парафин, срезы толщиной 10–15 μ окрашивали гематоксилин-эозином.

В литературе о патогенной роли различных триходин есть лишь отрывочные сведения. Некоторые авторы указывают на обильное слизеотделение при поражении кожи и жабр этими паразитами, но все эти наблюдения базировались только на клинической картине. Подробному изучению патогенной роли кругоресничных инфузорий посвящены работы Франка (Frank 1962) и Хайдера (Haider 1964).

На срезах установлена разница в локализации различных видов триходин на жаберном лепестке. Так, *T. mutabilis* и *T. nigra* прикрепляются к концам респираторных складок и обнаруживаются в больших количествах между жаберными лепестками в местах скопления форменных элементов и нитей фибрина. *T. epizootica*, как правило, располагаются между респираторными складками, с их боковых сторон. (Рис. 2, Табл. I 1, 5). Такая разница в локали-

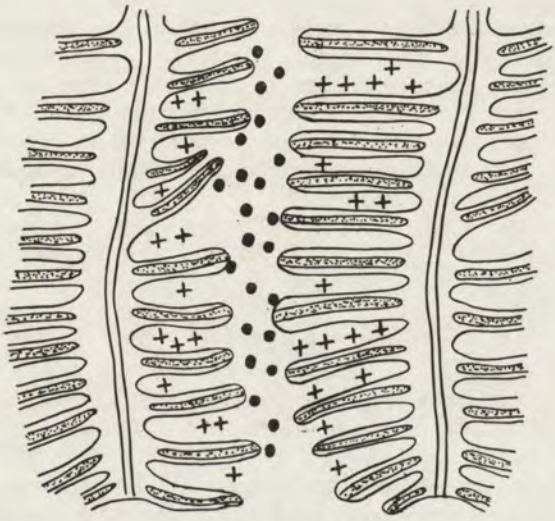

Рис. 2. Локализация *Trichodina mutabilis* (•) и *Trichodinella epizootica* (+) на жаберном лепестке

Fig. 2. The localization of *Trichodina mutabilis* (•) and *Trichodinella epizootica* (+) on the gill lobe

зации объясняется, на наш взгляд, невозможностью *T. epizootica* удержаться на концах респираторных складок, где они легко могут быть смыты током воды.

Различие между указанными выше видами триходин состоит не только в локализации на жаберном лепестке, но и в характере их патологического воздействия.

Наиболее сильные изменения жаберной ткани отмечены у сеголетков карпа при значительном поражении *T. mutabilis* и *T. nigra*. Инфузории, прикрепляясь к концам респираторных складок, нарушают целостность их эпителия. В местах прикрепления паразитов наблюдается кровотечение (Табл. I 2). Излившаяся кровь обнаруживается в виде скопления форменных элементов и нитей фибрина, вокруг которых располагаются в больших количествах инфузории. Отмечается гиперемия кровеносных сосудов. Паразиты вызывают деформацию эпителиальных клеток, частичную дезорганизацию респираторных складок, которые принимают вид колбообразных вздутий (Табл. I 3), встречающихся не только ближе к апикальным концам лепестка, но и по всему его протяжению. За счёт колбообразных вздутий увеличивается дыхательная поверхность жаберного лепестка, что является компенсаторной реакцией организма на нарушение дыхательной функции жаберного аппарата. В лепестке много ацидофильных клеток (Табл. I 4), которые от других клеток отличаются большими размерами

и крупными ядрами. Такие клетки наблюдал Андрес и Куражсковская 1963 у леща при экспериментально созданных условиях зимнего замора, Ланг (Lang 1965) у карасей при действии различных солей фенолов и других химических соединений. Можно наблюдать переход ацидофильных клеток в большие светлые клетки с бесцветной протоплазмой и ядрами, сдвигнутыми п перефирии. После выздоравливания наблюдается нормализация в строении жаберного аппарата: уменьшается число колбообразных вздутий и клеток с бесцветной протоплазмой.

Значительные изменения в жаберной ткани при поражении *T. epizootica* мы наблюдали у сеголетков пеляди. В местах прикрепления паразита развивается дегенерация и деформация эпителиальных клеток, диапедез эритроцитов. Характерно массовое слущивание клеток эпителия (Табл. I 5). В клетках появляются различные формы дегенерации ядра: кариорексис, пикноз и лизис. Следует отметить, что из трёх форм дегенерации ядра преобладает кариорексис, реже встречается пикноз и лизис.

У рыб старших возрастных групп изменения в жаберной ткани носят локальный характер.

Резюме

В прудовых хозяйствах средней полосы и юга СССР паразитируют у карпов и растительноядных рыб 6 видов триходин: *Trichodina domerguei* f. *acuta*, *T. pediculus*, *T. mutabilis*, *T. nigra*, *Trichodinella epizootica* и *T. bulbosa*. Из них *T. bulbosa* специфичен к растительноядным рыбам. *Trichodina domerguei* f. *acuta* и *T. pediculus* встречаются на коже и реже на жабрах, *T. mutabilis* и *T. nigra* чаще отмечаются на жабрах, а *Trichodinella epizootica* и *T. bulbosa* — формы жаберные. Жаберные формы триходин различаются между собой по локализации на жаберном лепестке: *T. mutabilis* и *T. nigra* прикрепляются к концам респираторных складок, а *T. epizootica* — с их боковых сторон.

Указанные виды паразитируют в разные сезоны года: *T. pediculus* — холоднолюбивая форма, встречающаяся зимой и ранней весной, *T. domerguei* f. *acuta* — в течение всего года, *T. epizootica* встречается с весны до осени. *T. mutabilis*, *T. nigra* и *T. bulbosa* — теплолюбивые виды, наибольшую интенсивность инвазии вызывающие в летнее время.

Патогенное влияние *T. mutabilis*, *T. nigra* и *T. epizootica* на ткани хозяина неодинаково. При триходинозе вызываемом *T. mutabilis* и *T. nigra* преобладают изменения эксудативного характера, а при триходинеллёзе, вызываемом *T. epizootica* — альтеративные процессы. Вызывая деструктивные изменения в жаберном аппарате, при высокой интенсивности инвазии, они составляют важный момент патогенного синдрома.

SUMMARY

In the fisheries of the middle part and the south of the USSR the following six species of Trichodins parasitize carps (*Cyprinus carpio*) and herbivorous fish (*Ctenopharyngodon idella*, *Hypophthalmichthis molitrix* and *Aristichtys nobilitis*): *Trichodina domerguei* f. *acuta*, *T. pediculus*, *T. mutabilis*, *T. nigra*, *Trichodinella epizootica* and *T. bulbosa*.

From these *T. bulbosa* is specific towards herbivorous fish. *Trichodina domerguei* f. *acuta* can be encountered on the skin and more seldom on the gills. *T. mutabilis* and *T. nigra* can be seen more often on the gills and *T. epizootica* as well as *T. bulbosa* are gill forms. The gill forms of Trichodins differ between each other by their localization on the gill lobe: *T. mutabilis* and *T. nigra* attach themselves to the tips of the respiratory fold and *T. epizootica* — their side parts.

The above mentioned species parasitize in different seasons of the year: *T. pediculus* — a cryophilic form that can be encountered in winter and early spring, *T. domerguei* f. *acuta* — during the whole year, *T. epizootica* can be seen from spring till autumn, *T. mutabilis*, *T. nigra* and *T. bulbosa* are the forms that display the greatest intensity of invasion during summer.

The pathogenic effects of *T. mutabilis*, *T. nigra* and *T. epizootica* on the tissues of the host is not the same. In the case of trichodiniosis caused by the changes that are exudative in character prevail and in the case of trichodiniosis caused by *T. epizootica* — alterative processes. By causing the ocurrence of destructive changes in the gill apparatus at high invasion intensity they consist an important factor of the pathogenic syndrome.

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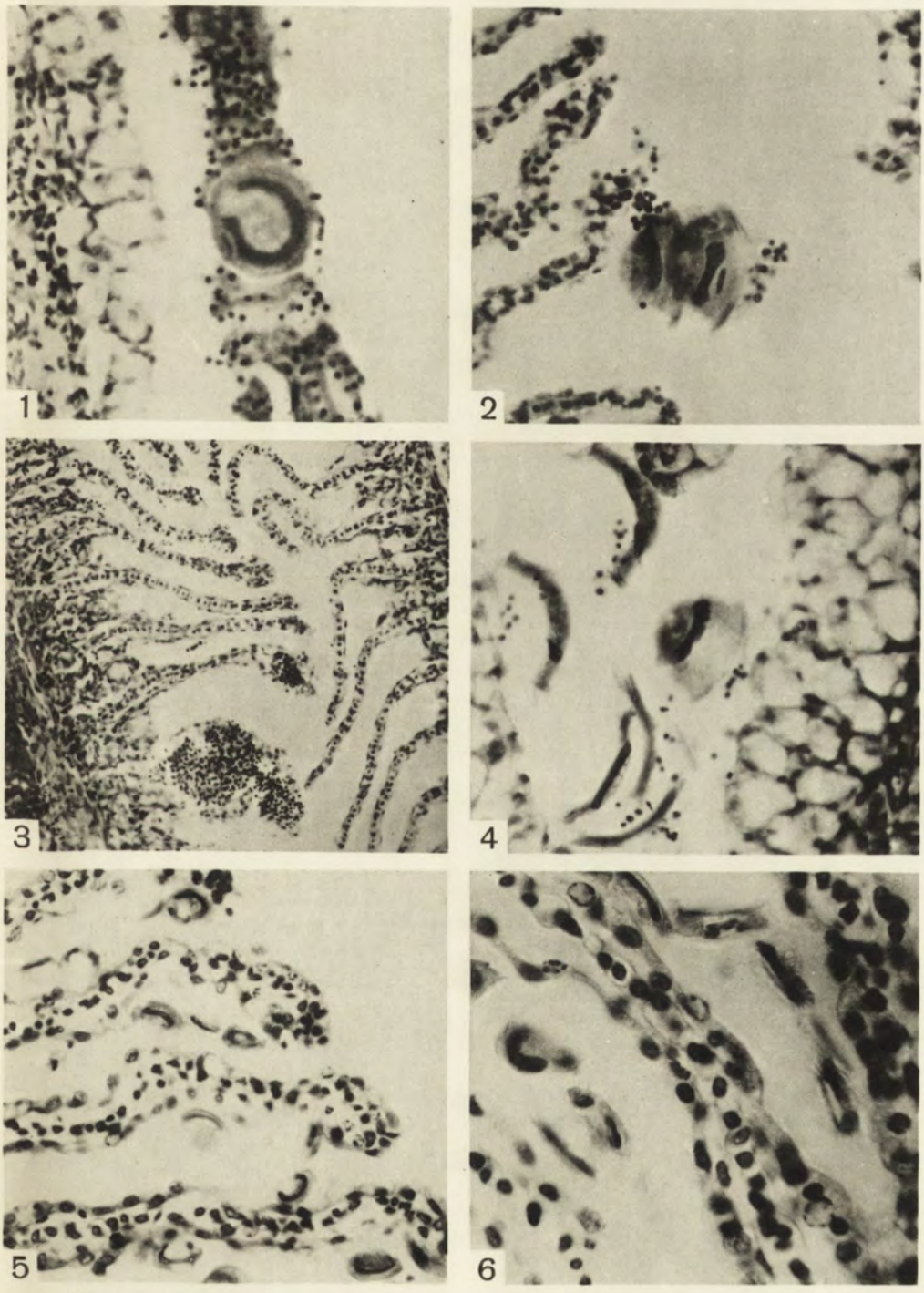
ПОДПИСИ К ТАБЛИЦЕ I

1: Локализация *T. nigra* на жаберном лепестке, 290 ×.
2: Кровотечение в респираторной складке (фиксация 4% формалином, окраска гематоксилин — эозином), 290 ×.
3: Колбообразные вздутия респираторных складок, 190 ×.
4: Ацидофильные клетки в жаберном лепестке, 290 ×.
5: Локализация *T. epizootica* на жаберном лепестке, 130 ×.
6: Слушивание клеток эпителия респираторных складок, 280 ×.

EXPLANATION OF PLATE I

1: The localization of *T. nigra* on the gill lobe, 290 ×.
2: The blood circulation in the respiratory fold (fixation in 4% formalin, staining with haematoxyline-eosine) 290 ×.
3: The bulb-formed interiors of the respiratory folds, 190 ×.
4: The acidophilic cells in the gill lobe, 290 ×.
5: The localization of *T. epizootica* on the gill lobe, 130 ×.
6: The scaling of cells of the epithelium of the respiratory folds, 280 ×.



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Longevity of microsporidian spores with special reference to *Octosporea muscaedomesticae* Flu*

Die Lebensdauer Microsporidia Sporen unter besonderer Berücksichtigung der *Octosporea muscaedomesticae* Flu

The longevity of a microsporidian in its extra-corporeal environment depends upon the ability of the spores to withstand a large number of interacting abiotic challenges including temperature, moisture, and solar radiation. Various abiotic and biotic components of the substrate in or on which the spores are found also influence longevity of the microsporidian in its resting form. Data pertaining to microsporidian spore life are important for they provide us with ecological information of interest to the protozoologist and the invertebrate pathologist. They also serve as practical guidelines for the successful maintenance of laboratory cultures of microsporidians for biological studies of various kinds. Assessment of spore persistence within the host's environment, as it relates to biological control, also rests upon a knowledge of spore longevity.

Review of microsporidian spore longevity

Published accounts of microsporidian spore life are very nearly limited to the much-studied honey-bee parasite *Nosema apis* and to species whose hosts are terrestrial phytophagous lepidopterans. For more than 95% of the known microsporidian species we have no information on the extent to which their spores withstand the vicissitudes of nature. Since microsporidians parasitize hosts having habitats ranging from strictly aquatic to purely terrestrial, one might well expect special adaptations in the ability of a given microsporidian to withstand the environmental challenges presented by the special features of its host's habitat. Whether this is the case remains to be demonstrated.

Aside from the living body of the host, the habitats of microsporidian spores may be grouped into four arbitrary though useful categories: 1. spores bound or covered in fecal deposits; 2. spores bound in host cadavers; 3. spores naked on dry surfaces (e.g., host feeding or working sites); and 4. spores naked in aqueous media. Data pertaining to the longevity of microsporidian spores has been summarized within these four working categories in Tables 1 through 4. It is important to note that environmental variables accompanying

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most accounts of spore life are expressed in very general terms and many estimates of longevity are probably minimal rather than maximal. Nevertheless, available evidence is substantial enough to permit some tentative conclusions.

Spores in fecal deposits

Moist fecal material serves as a substrate that supports luxuriant growth of saprophytic bacteria and certain microscopic fungi. The activities and metabolic products of these microbes apparently exert a deleterious effect on the microsporidian since its spore life is comparatively short under these conditions (less than 2 months). In relatively dry circumstances fecal deposits do not support a rampant proliferation of the microflora and microsporidian spore life is comparatively long (more than 1 year) (Table 1). Dried fecal material probably serves as a sealer that protects the microsporidian spore from excessive desiccation.

Table 1
Longevity records for microsporidian spores in fecal deposits

Species	Longevity*	Conditions of storage	References
Nosema apis	> 1 year	*Apis mellifera* feces on honey comb, 20°C and 50% R. H.	Bailey 1962
N. bombycis	< 2 mos.	Moist fermenting feces from larval *Bombyx mori*	Kudo 1930

* Based upon infectivity of spores ingested by susceptible hosts.

Spores in cadavers

The longevity of microsporidian spores within host cadavers held under moderate conditions of temperature and humidity exceeds one year for at least two species (Kudo 1930, Kulikov and Akramovsky 1961, (Table 2). Comparable longevity has also been reported for four other species whose dead hosts were held at moderate temperatures and high humidities (Weiser 1956). Data on one species suggests that moderate heat is detrimental to longevity while cooling seems to favor longevity (White 1919). For at least five species spore longevity in dead hosts held at moderate temperatures and humidities probably does not exceed two months (Allen 1954, Weiser 1956). Discrepancies between the results reported by Kulikov and Akramovsky (1961) and White (1919) may reflect inherent differences in the strains of *Nosema apis* studied.

Dry naked spores

The longevity records for naked and dry microsporidian spores under moderate conditions of temperature and humidity range from about two weeks (Allen 1954) to more than one year (Goodrich 1928) (Table 3). However, the bulk of the evidence suggests that the longevity of such spores does not exceed three or four months. A comparison of these longevity records with those reported for spores in dry feces or in host cadavers clearly indicates that naked spores are less able to resist the rigors of desiccation. The data also indicate that moderate heat tends to shorten longevity (White 1919) while cooling of naked spores increases longevity (Weiser 1956,

Kellen and Lindegren 1968). Differences between the results reported by Borchert and Polzin (1933) and White (1919) are probably due to minor variations in technique.

Table 2
Longevity records for microsporidian spores in host cadavers

Species	Longevity*	Conditions of storage	References
Nosema apis	4 1/2 yrs.	Dead *Apis mellifera* under room conditions	Kulikov et Akramovsky 1961
N. apis	1 mo.	Dead *A. mellifera* under room conditions	White 1919
N. apis	3 1/2 mos.	Dead *A. mellifera* under refrigeration	White 1919
N. apis	6 days	Dead *A. mellifera* under incubator conditions	White 1919
N. bombycis	> 1 year	Dead *Bombyx mori* moths under room conditions	Kudo 1930
N. destructor	18 days	Dead larval *Gnorimoschema operculella*, 27°C and 40–60% R. H.	Allen 1954
N. muscularis	2 mos.**	Dead lepidopterous hosts under dry room conditions	Weiser 1956
N. muscularis	> 13 mos.**	Dead lepidopterous hosts, room temps. and 80–90% R. H.	Weiser 1956

* Based upon infectivity of spores ingested by susceptible hosts.
** Similar findings reported for *N. lymantriae*, *Thelohania hyphantriae*, and *T. similis*, parasites of lepidopterans (Weiser 1956).

Table 3
Longevity records for naked microsporidian spores on dry surfaces

Species	Longevity*	Conditions of storage**	References
Nosema apis	> 3 mos.	Room conditions	Borchert and Polzin 1933
N. apis	< 2 mos.	Room conditions	White 1919
N. apis	15–21 days	Incubator temperature	White 1919
N. apis	7 mos.	Refrigerator temperature	White 1919
N. destructor	> 1 mo.	Room conditions	Steinhaus and Hughes 1949
N. destructor	15–16 days	27°C and 40–40% R. H.***	Allen 1954
N. muscularis	> 1 mo.****	Room conditions	Weiser 1956
N. muscularis	2–3 mos.****	0°C	Weiser 1956
N. plodiae	> 3 but < 4 mos.	6°C	Kellen and Lindegren 1968
N. plodiae	< 3 mos.	20–30°C	Kellen and Lindegren 1968
Perezia fumiferanae	> 30 but < 42 days	20°C	Thomson 1958
Thelohania muelleri	> 1 year	Room conditions	Goodrich 1928

* Based upon infectivity of spores ingested by susceptible hosts.
** On glass.
*** On potato tuber, not glass.
**** Similar findings reported for *N. lymantriae*, *Thelohania hyphantriae*, and *T. similis* (Weiser 1956).

Wet naked spores

Maximum longevity records for microsporidian spores are found in reports devoted to spore survival in aqueous media. From the standpoint of longevity under natural conditions these findings are probably of limited significance. However, they provide another dimension to our understanding of spore longevity and generally complement the evidence derived from other sources. That the longevity of some microsporidian spores may be as great as seven to ten years in a chilled clean aqueous medium has been demonstrated for two species (Revell 1960, Ohshima 1964) (Table 4). Among other species

Table 4
Longevity records for naked microsporidian spores in aqueous media

Species	Longevity*	Conditions of storage	References
Nosema apis	7 years	Clean distilled water, 5°C	Revell 1960
N. apis	6–10 days	Water and fermentative bacteria, room temperature	White 1919
N. apis	2 days	Water and fermentative bacteria, incubator temperature	White 1919
N. apis	7–9 days	Water and fermentative bacteria, refrigerator temperature	White 1919
N. apis	13–17 days	Water and putrefactive bacteria, room temperature	White 1919
N. apis	4 days	Water and putrefactive bacteria, incubator temperature	White 1919
N. apis	>3 mos.	Water and putrefactive bacteria, refrigerator temperature	White 1919
N. apis	2–4 mos.	In honey at room temperature	White 1919
N. bombycis	10 years	Ringer's solution, 2–5°C	Ohshima 1964
N. destructor	>6 mos.	Water, refrigerator temperature	Steinhaus and Hughes 1949
N. plodiae	>9 mos.	Water, 6 and 20°C	Kellen and Lindegren 1968
Perezia fumiferanae	2 1/2 mos.	Water, 5°C	Thomson 1958
P. fumiferanae	4–6 mos.	Frozen in water, at −5°C	Thomson 1958
Thelohania hyphantriae	3–4 mos.**	Water, 20°C	Weiser 1956
T. similis	>1 year	Water, 20°C	Weiser 1956
T. similis	>13 mos.***	Water, 0°C	Weiser 1956

* Based upon infectivity of spores ingested by susceptible hosts.
** Similar findings reported for *N. lymantriae* and *N. muscularis* (Weiser 1956).
*** Similar findings reported for *N. lymantriae*, *N. muscularis* and *T. hyphantriae* (Weiser 1956).

in similar media under the same conditions longevity clearly exceeds six months. That the acitivities of microflora sharing the aqueous medium decreases microsporidian spore longevity is also indicated, the harmful effects being more pronounced with increased temperatures (White 1919).

Miscellaneous factors and spore longevity

A significant but neglected physical factor that influences microsporidian spore longevity is solar radiation. The preliminary findings of White (1919) suggest that 24 hr of direct sunlight inactivate dry spores while wet spores are inactivated in about 35 hr under the same conditions. The extent to which heritable factors influence the longevity of microsporidian spores has also received little attention. In all likelihood the longevity of any microsporidian species could be increased by the selection and propagation of survivors after exposure to extreme environmental pressures. How a soil habitat influences microsporidian spore longevity also needs detailed investigation. Weiser (1956) suggests that spore survival in soil is similar to that for spores in host cadavers.

Octosporea muscaedomesticae: Spore longevity studies

Octosporea muscaedomesticae is a pathogenic microsporidian that lives within the epithelial cells of the proximal intestine of muscoid flies. Its spores are shed into the lumen of the host's intestine and voided with the feces. While spores are also found in the cadavers of host flies, fecal deposits are the principal extra-corporeal habitat of this species (Kramer 1968). Experiments performed for the purpose of determining the longevity of these feces-bound spores were executed in the manner described below. For comparative purposes naked spores held in water were also tested for longevity.

Materials and methods

Spores in Fecal Deposits: Clean glass slides were placed in cages of diseased flies. Within three to five days these slides were covered with spore-filled feces. One series of these feces-covered slides was placed in Petri dishes and refrigerated at 5°C. A second series of contaminated slides was held on a laboratory shelf at room conditions (22–27°C and 20–50% R.H.) in Petri dishes. At intervals indicated in Table 5, slides from each series were sprinkled with powered sucose and offered to hungry newly-emerged adult black blowflies, *Phormia regina*. The fecal deposits on some of the slides from the series held at room conditions were suspended in distilled water at the intervals given in Table 5 and offered to thirsty young adult *P. regina*.

Wet Naked Spores: Heavily parasitized proximal intestines were removed from adult *P. regina*. These intestines were ground in distilled water. The resultant homogenate was stored in a stoppered vial at 5°C. At intervals indicated in Table 5, samples of this spore suspension were offered to thirsty newly-emerged *P. regina*.

Examinations: The flies in all test groups were supplied with ample food and water following inoculation. After a twelve-day holding period at room conditions the ten flies in each test group or their cadavers were examined for *O. muscaedomesticae* infections. The findings are summarized in Table 5.

Results and discussion

A perusal of the data in Table 5 reveals that the longevity of feces-bound *O. muscaedomesticae* spores is influenced by temperature and moisture in various ways. Longevity extends to about 16 months for spores held at a constant low temperature (5°C) and 50% R.H. The life of spores held at more moderate but fluctuating conditions (22–27°C and 20–50% R.H.) is considerably shorter, i.e., about 8 months. That *O. muscaedomesticae* spore longevity under these conditions does not exceed 8 to 9 months is also suggested by the negative results obtained with spores dried for 271 to 340 days. The results obtained with dried feces-bound spores that were suspended in water indicate that moisture may have a deleterious effect on spore survival after two months. A microscopical examination of such spore preparations showed that the polar filaments of many spores were partially or completely evaginated. Thus environmental moisture may trigger a futile germination of the spore and thereby shorten spore longevity. How far one can extrapolate to nature

Table 5

Longevity of *Octosporea muscaedomesticae* spores as revealed by infectivity tests with spores of known ages

Age of spores in Days	Conditions of storage			
	Spores at 5°C in distilled water	Spores in Fecal Deposits		
		at 5°C and 50% R.H. offered dry	at room conditions offered dry **	at room conditions re-wet then offered**
1– 30	+*	+	+	+
31– 60	+	+	+	+
61– 90	+	+	+	0
91–120	+	+	+	0
121–150	+	+	+	0
151–180	+	+	+	0
181–210 (6 months)	+	+	+	—
211–240	+	+	+	—
241–250	+	+	+	—
251–260	+	+	+	—
261–270	+	+	+	—
271–280	+	+	0	—
281–310	+	+	0	—
311–340	+	+	0	—
341–370 (1 year)	+	+	—	—
371–400	+	+	—	—
401–430	+	+	—	—
431–460	+	+	—	—
461–490	+	—	—	—
491–590	+	—	—	—
591–690	+	—	—	—
691–790 (2 years)	+	—	—	—

* + — Spores produced infection when ingested by flies; 0 — no infection produced; — no test made.
** 22–27°C, 20–50% R.H.

from data gathered in the laboratory is impossible to state with certainty. However, the foregoing results suggest that *O. muscaedomesticae* spores may persist in the environment of the fly for many months under favorable conditions.

As can be seen in Table 5, *O. muscaedomesticae* spore longevity exceeds two years in cold distilled water. While the upper limits of spore longevity under these conditions was not established, it may approach the ten-year record for *Nosema bombycis* as given by Ohshima (1964). As he has noted psychrophilic fungi eventually grow in abundance if any organic debris is present in the aqueous storage medium. In my own studies, I have observed that adventitious fungal contaminants apparently inactivate *O. muscaedomesticae* spores within five years after storage in cold distilled water containing chunks of fly tissues. That microsporidian spores might be kept alive for more than ten years by controlling the tonicity of the storage solution as well as microfloral contaminants has been suggested by Ohshima (1964).

Summary

The longevity of spores of various microsporidian species and the conditions under which spores survive are reviewed. Available evidence suggests that: 1. differences in the ability to survive vary from species to species; 2. spores of some species bound in dried feces or in dried cadavers remain viable for one year or more under room conditions; longevity of other species under these conditions may be 3 months or less; 3. longevity of naked dried spores under room conditions generally does not exceed 3 to 4 months; for some species, however, longevity under these conditions ranges from about 2 weeks to over one year; 4. naked spores in a cold clean aqueous medium may survive for 7 to 10 years.

Studies on the longevity of *O. muscaedomesticae* spores indicate that: 1. feces-bound spores held at 5°C and moderate humidity remain viable for about 16 months; at room conditions such spores are viable for only about 8 months; 2. naked spores at 5°C in distilled water remain viable for at least 2 years; 3. environmental moisture may trigger a futile germination in previously dried spores and thereby shorten longevity. Other factors pertaining to microsporidian spore longevity are also considered.

ZUSAMMENFASSUNG

Untersucht wird die Lebensdauer verschiedener Microsporidia Gattungen und die Bedingungen, unter denen Sporen überleben. Das vorhandene Material lässt den Schluss zu, dass 1. Unterschiede in der Überlebensfähigkeit von Gattung zu Gattung variieren; 2. die Sporen bestimmter Gattungen, die in trockenen Exkrementen oder ausgetrockneten Kadavern eingeschlossen sind, unter Zimmertemperaturbedingungen ein Jahr oder langer lebensfähig bleiben können; die Lebensdauer anderer Gattungen unter diesen Bedingungen kann drei Monate oder weniger betragen; 3. die Lebensdauer schutzloser trockener Sporen unter Zimmerbedingungen gewöhnlich nicht drei oder vier Monate überschreitet; für einige Gattungen reicht die Lebensdauer unter diesen Bedingungen jedoch von etwa zwei Wochen bis zu über einem Jahr; 4. ungeschützte Sporen in einem kalten und sauberen wässrigen Medium können sieben bis zehn Jahre überleben.

Studien über die Lebensdauer von *O. muscaedomesticae* Sporen lassen den Schluss zu, dass 1. in Exkremente eingeschlossene Sporen, die bei 5°C und gemässigter Feuchtigkeit gehalten werden, etwa 16 Monate lebensfähig bleiben; unter Zimmerbedingungen beträgt die Lebensdauer dieser Sporen nur etwa acht Monate; 2. ungeschützte Sporen bei 5°C in destilliertem Wasser wenigstens zwei Jahre lebensfähig bleiben; 3. umgebende Feuchtigkeit ein fruchtloses Keimen in bis dahin trockenen Sporen auslösen kann und damit ihre Lebensdauer verkürzt. Andere Faktoren, die die Lebensdauer Microsporidia Sporen betreffen, werden ebenfalls behandelt.

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Mass accumulation of *Protozoa**

Massenakumulation der Protozoen

Euglena viridis, Euglena gracilis, Tetrahymena pyriformis and *Polytomella agilis* commonly form transient macroscopic aggregates of varying configurations (Wager 1911, Robbins 1952, Loefer and Mefferd 1952, reviewed by Gittleson and Jahn 1968 a). These aggregates arise after individual organisms are observed to actively swim upward and collect along a horizontal plane often near the medium air interface. The region of collection may also occur near the bottom of a young culture or at multiple sites at various heights in a heavily populated culture (Gittleson, unpublished observations). The active upward swimming of organisms which are heavier per unit volume than the medium is usually referred to as negative geotaxis. The mechanism of negative geotaxis remains an enigma (Kuźnicki 1968) but plays an integral role in the aggregating system described here.

In any case the organisms crowd closer and closer together until they begin to interfere with one anothers' normal movements. Then the cells notably tumble about in a disoriented fashion and at a critical density, they fall as aggregates, which in turn generate vertical columns (Gittleson and Jahn 1968 b). When the organisms reach bottom, they disperse and again swim upward perpetuating the cycle of vertical aggregate formation.

During our investigations of vertical aggregate formation, we observed that by reducing the surface area of cultures, the aggregating organisms would sediment in massive numbers. The following report concerns a quantitative evaluation of how cell number in the sediment is related to cell number at random and to cell volume of each species. An explanation for this mass accumulation effect is also put forward.

Methods

Throughout the experiments described here, cultures of *Polytomella agilis, Polytomella caeca, Euglena gracilis, Astasia longa* and *Tetrahymena pyriformis* were grown in 2000 ml Erlenmeyer flasks in 1000 ml batches and then transferred to 250 ml burettes for mass accumulation. In about 15 minutes the sedimented organisms were slowly withdrawn from the burette through a

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stopcock at the lower end (Plate I). All of these organisms were grown axenically on a medium consisting of 0.1 g sodium acetate, 0.2 g yeast extract and 0.1 g tryptone per 100 ml of glass distilled water at room temperature (23° to 26°C). Experiments were carried out on cultures in log phase of growth. Direct counts of cell number/ml were made using the Sedgewick-Rafter method (Scherbaum 1957). An estimate of cell volume was obtained on the basis that *Polytomella* spp. are nearly spherical and the other species resemble cylindrical bodies. Photographs of the aggregating organisms were made using Kodak high-contrast 35 mm film.

Results

Plate I is a photograph of *Polytomella caeca* vertical aggregates as they appear in the lower portion of a 250 ml burette. This is a typical view of the mass accumulation process for the other species discussed, too. Under dark-field illumination the aggregated columns of organisms appear white against a dark background. Some individual cells are swimming toward the surface in the dark areas between the columns. However, most of the population after about 15 minutes appears as a sediment of accumulated cells at the bottom of the burette. The area just above the stopcock is so packed with cells that it is opaque to light. Distance between the graduations denoting 10 ml levels actually measures 1.28 cm.

Generally, the total cell number/ml that accumulates in the sediment is directly related to the number of cells/ml at random in batch culture (Fig. 1 A). For example, *Polytomella caeca* grow to the largest random number in culture of 1.3 million cells/ml when concentration is greatest at 210 million cells/ml. If maximum relative concentration factor — RCF (cells/ml in sediment: cells/ml in batch culture) is used as a criterion for concentrating ability, then the species studied varied in their ability to concentrate in the following decreasing order: *P. caeca* (RCF, 259) > *P. agilis* (244) > *A. longa* (78) > *E. gracilis* (50) > *T. pyriformis* (39). It is important to note that the RCF ratio may be greater at lower cell numbers in batch culture because the relative rate of increase in this number exceeds that of increasing cell number in the sediment. In the case of *P. caeca*, as the cell number in batch culture doubles from 600 000 to 1.2 million (a 100% increase), the cell number in the concentrate increases only about 34% from 150 to 210 million cells/ml.

Figure 1 B indicates that maximum accumulations for each genera are dependent upon cell volume. There is an inverse relationship between mean cell volume and cell number/ml of concentrate in the same order found for relative concentrating capacity. More *Polytomella* will pack into a given volume than *Tetrahymena*. Although *P. caeca* has the greater concentrating ability, *P. agilis* did attain the highest cell number/ml in the concentrate which may be related to slight differences in their volumes.

Discussion

Significantly, no special input of energy from centrifugal forces, electrical currents, or chemical gradients are necessary to bring about these accumulations. The energetics for mass accumulation are derived from the process

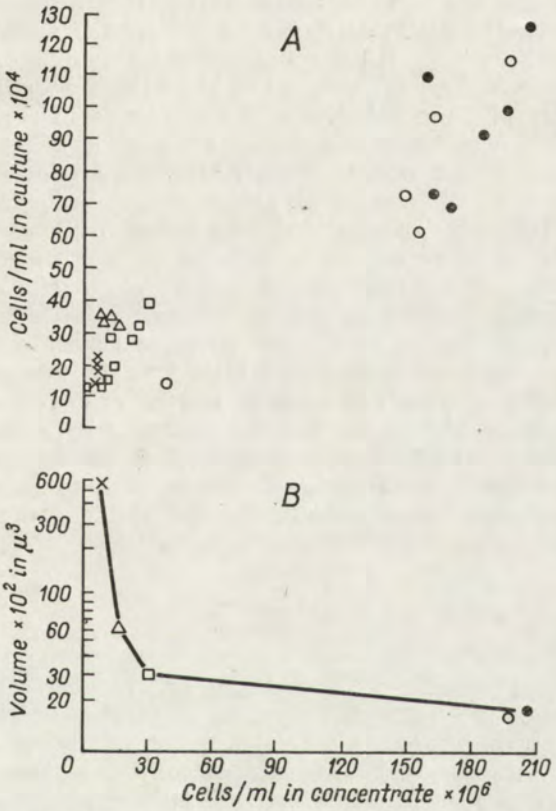

Fig. 1. Relationship between A cell number/ml in culture to cell number/ml in the concentrate; and B cell volume to cell number/ml in the concentrate for ● *Polytomella agilis*, ○ *Polytomella caeca*, □ *Astasia longa*, △ *Euglena gracilis*, × *Tetrahymena pyriformis*

whereby microorganisms swim upward and collect near the surface of the medium commonly referred to as negative geotaxis. When the organisms can no longer maintain their surface positions due to overcrowding, they fall as aggregates which in turn generate vertical columns. The number of columns formed are directly related to surface area. Each vertical column can contain only a maximum number of cells and so any additional organisms sediment without returning to the surface. Thus, when the number of cells/ml is kept constant and the surface area is decreased, only a fraction of the cells can take part in the aggregating process. For example, at least 100 columns are evident in a large surface area Erlenmeyer flask culture but only a few columns are observed in a burette.

Theoretically, spherically-shaped *Polytomella agilis* with a diameter of 10 μ could accumulate to one billion cells/ml when they are packed to the point of touching each other (this calculation is based upon the equation that distance between two spheres from center to center is equal to the cube root of 1/cell number). Realistically, the flagella of about body length even without

full extension would add to the effective size of *P. agilis*. If we estimate that the overall diameter of the *P. agilis* body plus flagella is 15 μ, then according to the equation above 295 million cells/ml could accumulate. This last figure is very close to the highest cell number of 210 million actually counted in the sediment. Conceivably, the effective cell diameter is in fact closer to 16.5 μ which would limit packing of *P. agilis* to 210 million cells/ml. This analysis should apply equally well to cells of other body shapes and volumes.

Mass accumulation described here could be used economically on a large scale to harvest food for oysters and shrimp larvae in the aquaculture process (Bardach 1968, Webber 1968) or even in the diet of adult animals. We have fed goldfish exclusively on concentrated *Polytomella agilis* for over a month. The goldfish quickly learned to recognize the pipette and to stick their mouths above water to receive the drops of concentrated cells.

We have also observed that *Polytomella* spp. in the concentrate begin breaking-up within an hour and after a day the preparation is nearly cell-free. Isolated flagella with kinetosomes attached are especially noted soon after the organisms have been accumulated. This process may be useful as a very gentle mechanical method for disrupting cells to obtain their isolated organelles. Mass accumulation should be applicable for many species of protozoa that commonly form vertical aggregations.

Summary

A new method is described for obtaining cell numbers of microorganisms up to approximately 260 times that available at random in log-phase cultures. Maximum concentration capacity is related to cell number/ml in batch culture and to volume of the species. The ease of collecting these masses of cells suggests its value as a food source and in experiments requiring the gentle collection of large numbers of cells and their organelles.

ZUSAMMENFASSUNG [1]

Es wird eine neue Methode beschrieben, die es ermöglicht, annähernd das 260-fache an Mikroorganismen (Protozoen) der Dichte zù erhalten, wie sie gewöhnlich in Kulturen mit logarithmischer Wachstumshpase auftreten. Die maximal mögliche Konzentration wird bezogen auf die Anzahl Zellen/ml Batch-Kultur und auf die Zellgrösse der entsprechenden Art. Die Einfachheit der Methode, diese Massen an Zellen heranzüzihen, lässt deren Wert als Nahrungsmittel vermüten. Ebenfalls scheint diese Methode wertvol für Experimente, die schnell eine grosse Anzahl von Zellen und deren Organellen erfordern.

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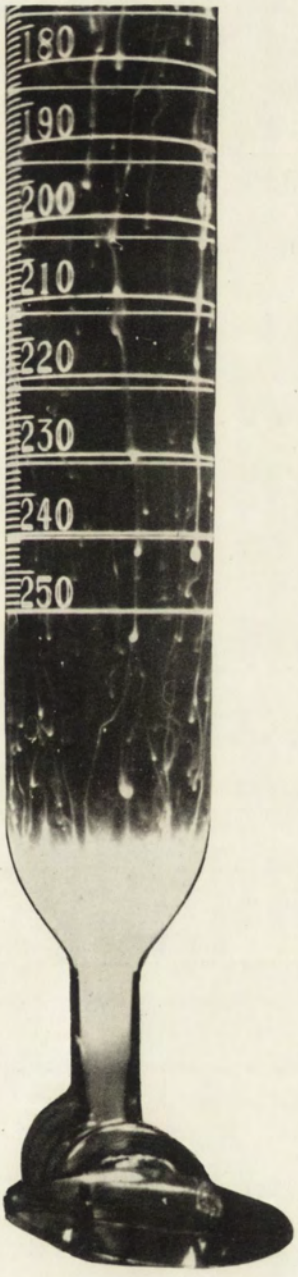
EXPLANATION OF PLATE I

1: A photograph of *Polytomella caeca* accumulating at the bottom of a 250 ml burette just above the stopcock. Distinct vertical aggregates can be observed above the sediment. Distance between the graduations denoting 10 ml levels is 1.28 cm



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