STUDIES ON THE EVOLUTION OF THE OPHRYOSCOLECIDAE (CILIATA: OLIGOTRICHA)

by

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FOREWORD

The present paper was started as an investigation into the parallel variability of two species of *Entodinium* related to *E. caudatum*. It has shown, that all these species produce sets of forms with the "*caudatum*", "*loboso-spinosum*" and "*dubardi*" types of the caudal spination. It became obvious, that in the literature the specific names of *E. caudatum*, *E. loboso-spinosum* and *E. dubardi* were used to designate assemblages of parallel forms belonging to different species of *Entodinium*.

The transformation of the left lateral groove into a narrow furrow and the trend to ventrad displacement of the contractile vacuole in *E. simulans* sp. n. lead to the unorthodox comparison of the "left" body-side of *Entodinium* with the "right" body-side of *Diplodinium*. This resulted in the discovery of the rôle of torsional displacement of structures in the origin of the higher Ophryoscolecidae and lead to a revision of some basic concepts of the comparative morphology of this family.

An analysis of generic characters of the Ophryoscolecidae from the standpoint of the theory of torsional displacement of structures resulted in the reconstruction of the phylogeny of this family and in the establishment within it of three new subfamilies.

PART I

NEW SPECIES OF *ENTODINIUM* WITH THE "*CAUDATUM*", "*LOBOSO-SPINOSUM*" AND "*DUBARDI*" FORMS AND SOME EVOLUTIONARY TRENDS IN THE GENUS *ENTODINIUM*.

> "Distinct species present analogous variations; and a variety of one species often assumes some of the characters of an allied species, or reverts to some of the characters of an early progenitor"
>
> Charles Darwin, *The Origin of Species*, 1859.

1. Introduction

The present paper originated as the result of unexpected difficulties, experienced by the author in identifying some forms of *Entodinium* with caudal spinations similar to that of *E. caudatum* and *E. loboso-spinosum*. The new forms, found in the rumen-contents of domestic sheep and goats of Western Punjab, were easily identifiable with the aid of Dogiel's key to the genus *Entodinium* (Dogiel, 1927). The result was, however, unexpected and somewhat discouraging, as the author was compelled, strictly following Dogiel's key, to identify three obviously different species of *Entodinium* as *E. caudatum*, and three corresponding forms with another type of the caudal spination -- as *E. loboso-spinosum*. It became clear, that the structure of the caudal spination is not a reliable guide to the identification of species related to *E. caudatum*. It was obvious, that the identification and description of the new forms was made difficult on one hand by the inadequacy of descriptions of some species of *Entodinium*, including *E. caudatum*, and on the other hand by the high environmental variability of this species (see Poljansky and Strelkow 1934, 1938 and Strelkow and Poljansky 1937). A deeper insight into the history of examination of *E. caudatum* and of related forms became therefore a necessity.

E. caudatum was described by Stein in a paper read before the Royal Society of Czekia on the 8th of March, 1858 and published in the proceedings of this Society in 1859. The presence of two data, associated with the description of *E. caudatum* and with the establishment of the genus *Entodinium* -- that of reading the paper and of its publication in the proceedings -- resulted in confusion as to the year of description of this species and genus. Thus, e.g., Dogiel (1927) in his well-known monograph of the family Ophryoscolecidae gives two different data of its description: 1858 (l.c., p. 35) and 1859 (l.c., p. 61). Kofoid and MacLennan (1930, p. 496) give this year as 1858, whereas Bush and Kofoid (1948, p. 245) give it as 1859. Crawley (1923, p. 395), Bhatia (1936, p. 277), Poljansky and Strelkow (1938, p. 9) give this datum as 1859. According to the rules of zoological nomenclature the presentation of a paper before a meeting does not constitute a publication. Therefore the correct datum of description of *E. caudatum* (as well as of the genus *Entodinium*) is 1859.

Stein's description of *E. caudatum* runs as follows: "*Entod. caudatum* zeichnet sich durch einen flachgewölbten, muschelartigen Körper aus, dessen einer Seitenrand nach hinten in einen langen gedrehten, schwanzartigen Stachelvortsatz ausläuft, während der andere Seitenrandt hinten in zwei kurzen, zahnförmigen Spitzen endet" (Stein 1859, p. 58). (It has to be noted, that what Stein described as lateral side with the spine-shaped appendix is designated by later authors as dorsal side. Aut.) Thus Stein's description of E. caudatum is limited to the characters of the caudal spination only. Such features as the position of the contractile vacuole and the development and shape of the left lateral groove are not mentioned by Stein. His description of E. caudatum is not accompanied by drawings. The second paper of Stein (1859b), concerned with rumen ciliates, has added nothing to this description. Later Schuberg (1888) redescribed E. caudatum and gave good drawings of it (l.c., plate 12, Figs. 7 and 8. Fig. 8 reproduced by Doflein 1931, p. 1196; see also Fig. I of the present paper). The specimens, depicted by Schuberg, have a very long lateral groove, a contractile vacuole situated near the ventral body-side, ventrally to the left lateral groove (according to Schuberg's nomenclature the contractile vacuole is situated near the right side of the body). Conspicuous in Schuberg's figures of E. caudatum is the length of the dorsal spine, which is equal to the body length of the depicted specimens. A similar specimen of E. caudatum was depicted by Fiorentini (1889) in his Fig. 4 of plate 4.

Dogiel (1927), in his monograph of the family Ophryoscolecidae, described E. caudatum Stein with a contractile vacuole near the dorsal side close to the anterior end of the macronucleus (see Fig. II). He believed this species to be conspecific with E. caudatum Stein sensu

Schuberg, and surmized that this last author had erroneously depicted the vacuole as being situated near the ventral surface of this ciliate.

A few years later Kofoid and MacLennan (1930) described two new species of *Entodinium* -- *E. laterale* and *E. rectangulatum* -- with caudal spination similar to that of *E. caudatum* Stein but with the contractile vacuole situated "in middle of left side" of the body and projected in side-view on the anterior part of the oesophagus (Fig. III). The situation of the vacuole in these two species of *Entodinium* is thus intermediate between that in *E. caudatum* Stein *sensu* Schuberg and in *E. caudatum* Stein *sensu* Dogiel. The shape and development of the left lateral groove in *E. laterale* and *E. rectangulatum* was neither described nor depicted by Kofoid and MacLennan, who adhered to the accepted custom of depicting *Entodinium* from the right side. On the basis of the peculiar position of the contractile vacuole in *E. laterale* and *E. rectangulatum*, Kofoid and MacLennan have separated these two species into the "*laterale*" group of *Entodinium*. They presumed that these species originated "from *E. caudatum*, or a similar form, by a change in the position of the contractile vacuole" (l.c., p. 519).

The variability of *E. caudatum* and of some other species of the Ophryoscolecidae was studied experimentally in clones by Dogiel's pupils -- Poljansky and Strelkow (1934, 1938) and Strelkow and Poljansky (1937). In their paper of

Ventral side
(Right side
according to
Schuberg)

Dorsal side
(Left side
according to
Schuberg)

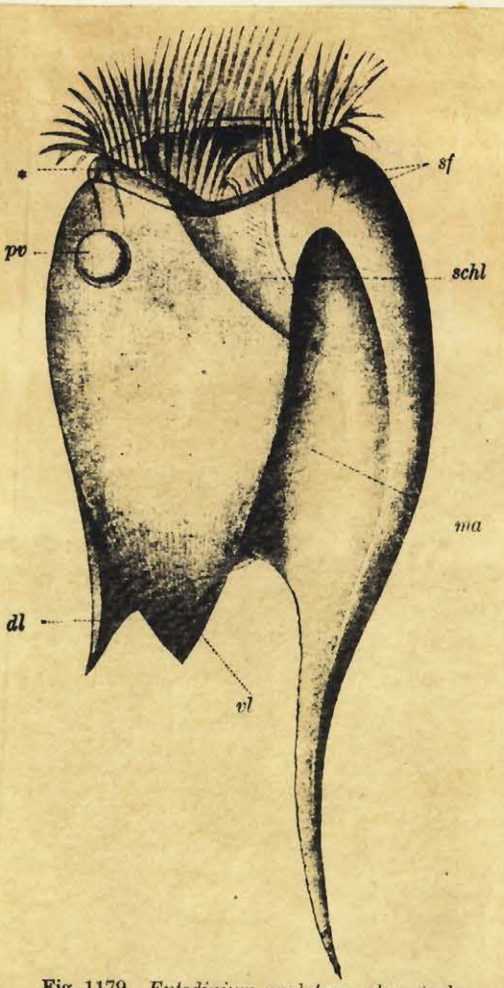


Fig. 1179. *Entodinium caudatum.* *vl* ventraler, **dl** dorsaler Lappen, *ma* muschelförmige Aushöhlung, **pv** pulsierende Vakuole, *schl* Schlund, *sf* Spiralfalte, * Stelle, wo die Cirrenreihe beginnt. (Nach Schuberg.)

Fig. I

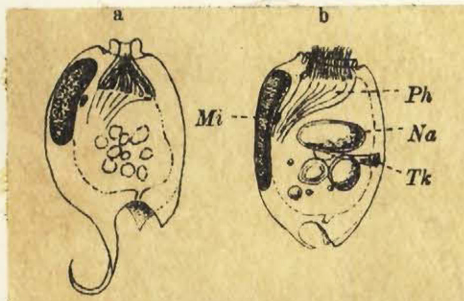


Fig. 28. *Ent. caudatum.*
a mit normal, b mit schwach entwickeltem dorsalen Stachel.

Fig. II

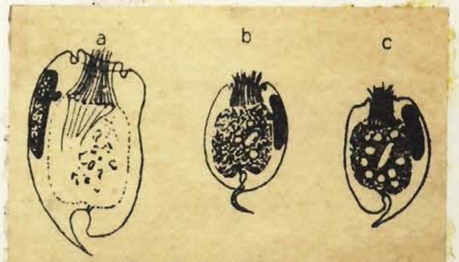


Fig. 27. ***Ent. loboso-spinosum.***
a vom Schaf, b und c von der Antilope *Bubalis cokei.* a von der rechten, b u. c von der linken Seite gesehen.

Fig. IV

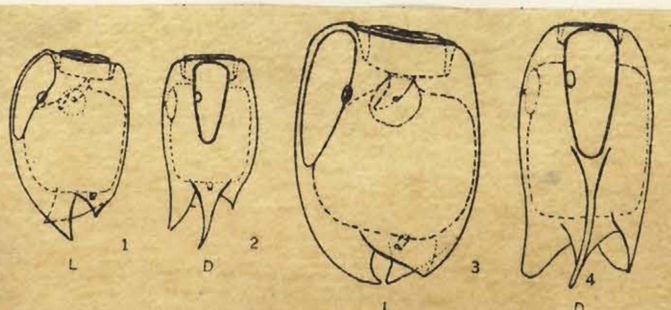


Fig. L. *1* and *2*, *Entodinium laterale* sp. nov., × 750; *3* and *4*, *Entodinium rectangulatum* sp. nov., × 750. *D*, dorsal view; *L*, lateral view.

Fig. III

1938 these authors have thoroughly redescribed E. caudatum Stein and have given the characteristics of two races of this species, designated by them as races "A" and "B". The individuals of the race A are larger than those of the race B and have a better developed caudal spination. The most conspicuous morphological character by which these two races can be differentiated is the broadness of the base of the right ventral lobe in race A, this base extending over 1/3 of the circumference of the body. In race B the base is narrow and the right lateral lobe has the shape of a pointed narrow triangle (l.c., p. 12, Fig. 11). These differences are similar to those existing between E. rectangulatum and E. laterale of Kofoid and MacLennan, the first species resembling in the structure of the right ventral lobe the race A, the second species -- the race B.

Poljansky and Strelkow have shown, that both these races of E. caudatum are environmentally plastic and undergo considerable morphological changes under the influence of the diet of the host. They studied this influence experimentally in clones, derived from typical specimens of E. caudatum with well developed caudal spination. The clones were established in goats and sheep kept on a mixed diet of herbage and oats. One to six weeks after the establishment of the clone, E. caudatum exhibited wide variation in the development of the caudal spination. Individuals with spination, typical of E. caudatum were present together with specimens with rounded posterior end, deprived of spines and lobes. The variability was continuous, the above mentioned extreme variants being connected by transitional forms. Poljansky and Strelkow distinguish 6 classes of forms in these continuous series of variation. Individuals of class 1 have a well developed caudal spination, typical of E. caudatum, consisting of a long dorsal spine and well developed left and right ventral lobes. Individuals of class 2 differ from those of class 1 only in the shortness of their dorsal spine which is not longer than 10µ. Class 3 is characterized by the rounding up of tips of both ventral lobes. The individuals of this class may possess a dorsal spine and are then classified as typical class-3 individuals, or lack this spine, in which case they are designated as individuals of class 3a. Specimens of class 4 lack the right ventral lobe, but possess a well developed left ventral lobe and dorsal spine. The caudal spination of these forms is thus similar to that of E. loboso-spinosum Dogiel 1927 (see Fig. IV). In individuals of class 5 the dorsal spine and the ventral lobes are very short. In specimens of class 6 the caudal spination is completely absent. Individuals of this class are, according to Poljansky and Strelkow, indistinguishable from E. simplex Dogiel 1925 (see Fig. V).

Fig. V. Classes of forms of Entodinium caudatum.
(After Poljansky and Strelkow, 1938)

The relative frequency of individuals of different classes was shown to be dependent on the diet of the host: when the host animal was fed on herbs and hay, forms of the 5th and 6th classes prevailed. When the food was rich in starch, forms of the classes 1 and 2 were prevalent. It has to be noted, that forms of class 4 -- those similar to E. loboso-spinosum -- were always scanty, comprising usually 1-6 per cent of the total number of individuals and, in the experiments of Poljansky and Strelkow, have reached 12 per cent only on one occasion.

Another factor influencing the variability of E. caudatum was shown to be the presence of predators (Strelkow and Poljansky, 1937). When the predatious E. vorax was introduced into a faunule, consisting of a clone of highly variable E. caudatum, it eliminated all the spineless individuals of the last species, leaving a population composed exclusively of long-spined forms of class 1.

The experiments of Poljansky and Strelkow have shown, that features, described by Stein as specific characters of E. caudatum -- the structure of the caudal spination -- are environmentally variable, the food-induced polymorphism of this species covering a range of characters, proper to several species of Entodinium. Whereas the individuals of class 1 have a caudal spination described by Stein (1859a) as typical of E. caudatum, those of class 4 possess a spination typical of E. loboso-spinosum Dogiel, and those of class 6 closely resemble some tailless species of Entodinium.

Soon after the publication of the preliminary communication of Poljansky and Strelkow (1934) there appeared a trend in the literature to regard E. loboso-spinosum and E. simplex as designations for variants of E. caudatum and, therefore to synonymize them with this last species (see e.g., Wertheim, 1935). Later, however (1938), Poljansky and Strelkow have shown that the species, identified by them as E. simplex Dogiel, does exist as a separate species which is not able to produce tailed individuals under any known conditions. It is highly probable also, that *E. loboso-spinosum* Dogiel is not simply a designation for variants of *E. caudatum* belonging to the 4th class of Poljansky and Strelkow's classification, as these individuals, although similar in their caudal spination to Dogiel's *E. loboso-spinosum*, differ from this last species in their habitus. Moreover, they are comparatively rare variants in an obviously continuous series of variation, never occurring in considerable numbers. It is hard to believe that Dogiel could have described such variants as a good species. Moreover, Dogiel's description of *E. loboso-spinosum* does not mention the position of the contractile vacuole which is also not depicted in his figures of this species. These figures (Dogiel, 1927, p. 60, Figs. 27a-e) may represent an assemblage of forms, belonging to different species, but possessing a common type of caudal spination (see Fig. IV on p. 7).

Forms of *Entodinium*, found in my material, were characterized by the caudal spination similar to that of *E. caudatum* Stein and *E. loboso-spinosum* Dogiel but possessed, as a constant character, a lateral contractile vacuole characteristic of the "*laterale*" group of *Entodinium* of Kofoid and MacLennan (1930). Corresponding tailless forms with lateral position of contractile vacuoles, connected to the "*loboso-spinosum*" forms by transitional variants, were also present. On the other hand *E. caudatum* Stein *sensu* Dogiel (with the vacuole adjacent to the macronucleus)was found only in one faunule. This made possible the examination of the variability of the new forms, labelled by the lateral position of their vacuoles. In this paper an attempt is made to describe these forms and to discuss their relationships.

2. Materials and Methods

The material -- rumen contents of 68 Jamnapari goats and of 59 sheep -- was collected in the butchery in Rawalpindi - Cantonment, Western Pakistan, in the period between April 1950 and June 1954. The collection had to be done at night-time, as the usual time of butchering in Pakistan is about midnight in summer and between 8 and 10 p.m. in winter. The technique of collection was as follows: the rumen contents were thoroughly mixed inside the intact rumen of the freshly slaughtered animal and a cut 3-4 inches long was made in its wall. A wide-meshed tea-strainer was pressed against the cut and the fluid penetrating into the sieve collected into a wide-mouthed pipette. The gastric contents were mixed with an equal volume of 20 per cent formalin, the resulting mixture thus containing about 3.8-4.0 per cent formaldehyde.

The material for temporary mounts was stained with Weigert's iodine. In preparing permanent slides Westphal's method (1934), modified by the author, was used: a few drops of material which were previously well shaken were introduced into a centrifuge tube filled with distilled water and the tube centrifuged at about 600 rotations per minute for 3 minutes. The supernatant fluid was discarded and the sediment washed again in a fresh portion of distilled water. After the second centrifuging the sediment was mixed with an equal volume of human serum. A drop of suspension was placed on a slide and spread to the size of a circle of about 18-20 mm. in diameter. The slides were placed in horizontal position in a glass jar containing cotton, soaked in undiluted formalin. In about 18-20 hours the films were coagulated, but even a 3-4 day long stay in formalin vapors did not damage the material. The coagulated films were hardened for 10 minutes in 70 per cent alcohol, rinsed in water and stained with Heidenhain's iron haematoxylin or Ehrlich's haematoxylin, Mayer's acid haemalum in Hoare's modification (Hoare, 1949) or with Gower's carmin (Gower, 1939), A few films were counterstained with orange G. The best results were obtained with Mayer's haemalum and Gower's carmin. Drawings were made with the aid of a camera lucida or a drawing prism.

3. Terminology

A few words have to be added concerning the morphological terminology, used in the present paper; it is identical to that of Dogiel, Kofoid and MacLennan and other recent authors. It has to be emphasized, however, that earlier authors, particularly Stein (1859a and b) and Schuberg (1888) used a different terminology. Thus Schuberg designated the nuclear body-side of *Entodinium* as left side, whereas at the present time it is designated as dorsal side. It is obvious that formally identical statements, e.g. "The caudal spine of *E. caudatum* is bent to the left" have different meanings when used by Schuberg on the one hand, and by a contemporary author on the other.(see Fig. I, p. 7).

At the present time the term "body length" designates the distance from the anterior pole of the body to the anal opening, but in the paper of Schuberg, published in 1888, it meant the distance from the anterior pole to the end of the longest caudal spine. Thus the length to width relation, deduced from measurements given by Schuberg, can not be directly compared (as Dogiel did in his monograph, p. 62) with the length to width relation based on the modern way of measuring. These differences have to be kept in mind by everybody interested in the old literature on Ophryoscolecidae.

In the present paper the terms "*caudatum-*", "*loboso-spinosum-*" and "*dubardi-*"types will be used to designate forms of Entodinium produced by the intra-specific variability within different species of this genus. The term "caudatum-" type will be used to designate variants with one dorsal spine and two ventral lobes similar in the development of the caudal spination to E. caudatum as described by Stein (1859a), Schuberg (1888) and Dogiel (1927). By the term "loboso-spinosum"type will be designated variants with one dorsal spine and only one -- the left -- ventral lobe, thus similar in the type of their caudal spination to E. loboso-spinosum Dogiel. Tailless variants, similar to E. dubardi Buisson 1923, will be designated as the "dubardi-"type.

E. dubardi is characterized by the length to depth relation not exceeding 1.55, and so are the tailless variants, described in the present paper. We have not found tailless individuals with length to depth relation of over 1.7 (which according to Dogiel is characteristic of E. simplex) and find therefore the term "simplex-"type to be inappropriate for their designation.

Species and forms of Entodinium, described in the present paper, are obviously closely related both to E. caudatum and to species of the "laterale" group of this genus in the sense of Kofoid and MacLennan. All these forms, including E. caudatum, will be referred to in the present paper as forms of the "caudatum-laterale" group of Entodinium.

The following forms of Entodinium of this group were found in our material:

4. Entodinium rectangulatum
Kofoid and MacLennan 1930
forma caudatum f. nova (Figs. 1 and 2)

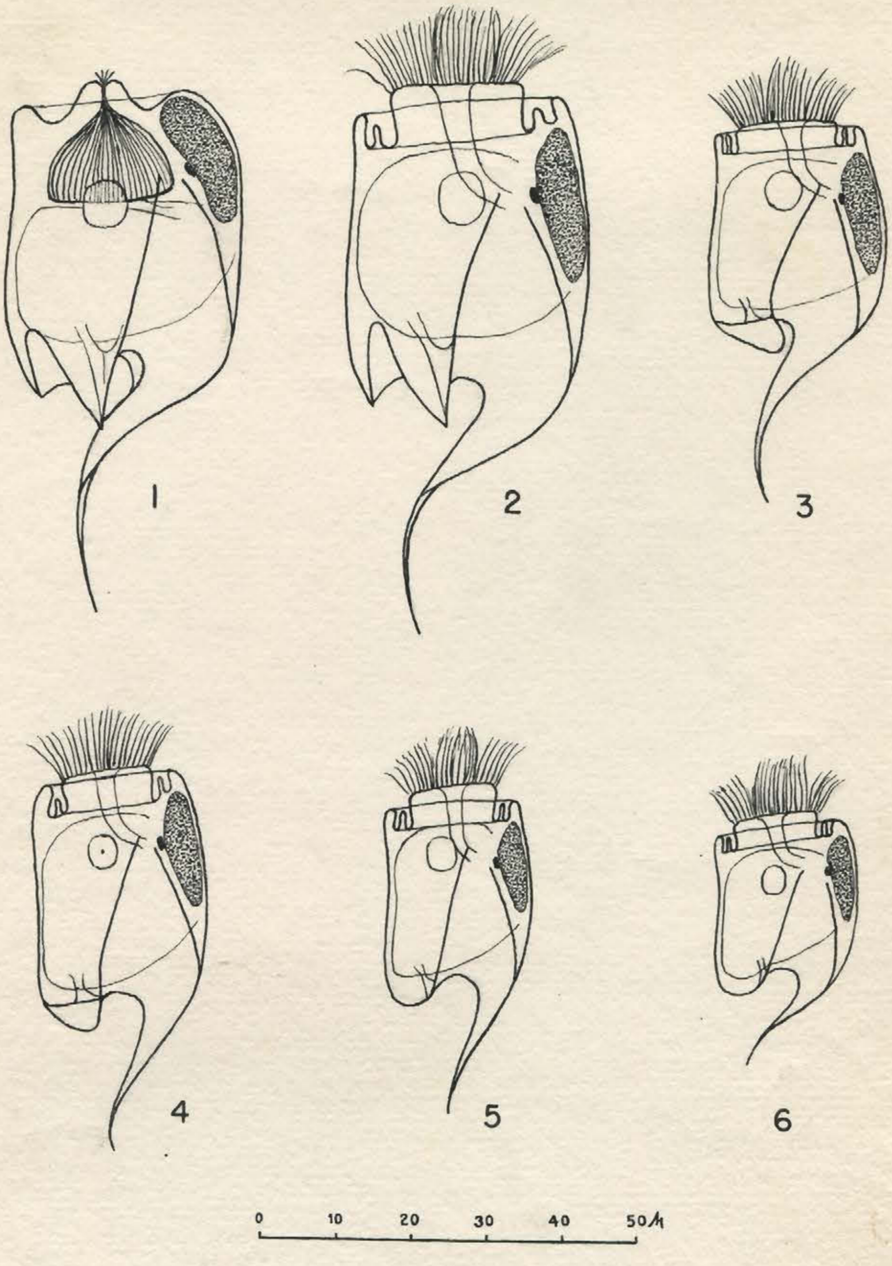
Diagnosis: Body nearly rectangular in side-view, 35 (23-47)µ long and 29 (23-39)µ deep. Contractile vacuole on the middle line of the left side of the body on the level of the micronucleus ventrally to the broad left lateral groove. Two ventral lobes and one dorsal spine. Dorsal spine approximately as long as the dorso-ventral diameter, with a laterally compressed basis and a long and narrow distal part. Left ventral lobe fleshy, triangular, with the anal opening at the base of its mediodorsal surface. Right ventral lobe forming a thin plate with a nearly rectangular apex.

Type host: domestic sheep.

Type locality: Rawalpindi, W. Pakistan. Collected in June 1951.

Measurements, shown in Table I, are based on 100 specimens from the rumen of sheep 48. The ciliates measured were stained with Mayer's acid haemalum and mounted in Canada balsam.

Description: Body nearly rectangular in side-view, 1.16 (0.9-1.5) dorso-ventral diameters in length (see Figs. 1 and 2). Oral area set nearly at right angles to the main body-axis. Ventral surface nearly flat, dorsal slightly convex, more so in its posterior part. Posterior end truncated at right angles. The base of the dorsal spine



Figs. 1 and 2 -- Entodinium rectangulatum forma caudatum, forma nova.

(Fig. 1 -- contracted specimen; Fig. 2 -- expanded specimen).

Figs. 3 to 6 -- E. cf. loboso-spinosum Dogiel 1927.

All specimens from the faunule of sheep 48.

TABLE I

Dimensions in μ of E. rectangulatum f. caudatum from the rumen of sheep 48, based on measurements of 100 specimens mounted in Canada balsam.

	M ± m	σ	V(%)	Observed limits of variation
Length	34.62 ± 0.44	±4.42	12.77	23.0-47.0
Dorso-ventral diameter	29.23 ± 0.31	±3.06	10.46	23.0-39.0
Relative length	1.16 ± 0.01	±0.12	10.04	0.9-1.5
Length of macronucleus	21.32 ± 0.38	±3.80	17.87	11.0-31.0
Diameter of oral disc	16.74 ± 0.26	±2.62	15.78	10.0-24.0
Length of dorsal spine	35.09 ± 0.39	±3.85	10.99	26.0-44.0
Length of left ventral lobe	11.24 ± 0.19	±1.85	16.44	7.0-17.0
Length of right ventral lobe	8.69 ± 0.15	±1.48	17.03	4.0-14.0

set in sagittal plane, laterally compressed and plough-shaped; its distal part produced in a long, narrow, flexible thorn. The length of the dorsal spine equal to or longer than the dorso-ventral diameter (depth), and usually equal to the body length. Left ventral lobe fleshy, triangular, with an acute apex. Anal opening situated at the base of its mediodorsal surface, and continuing in caudal direction as a shallow furrow running along the mediodorsal surface of the left ventral lobe and nearly reaching its apex. The right ventral lobe is a thin plate with a nearly rectangular tip.

Left lateral groove triangular with its apex situated between the micronucleus and the contractile vacuole just posterior to the base of the outer adoral lip. The ventral boundary of the left lateral groove is formed by the dorsal edge of the left ventral lobe and a fold on the left lateral surface of the body which is the anteriad extension of this edge. The dorsal boundary produced by a cuticular fold running close to the left ventral side of the nuclear apparatus from the base of the outer adoral lip caudad and reaching the dorsal side of the base of the dorsal spine on the level of the anus (Figs. 1 and 2). The base of the triangular left lateral groove, which is produced by a line connecting the anus with the dorsal edge of the dorsal fold on the level of the anus, usually equals half of the dorso-ventral diameter.

The mouth is an ellipsoidal opening with its long axis set transversally. The oesophagus is situated to the right from the anterior pole of the endoplasmic sac. It is bent dorsad and terminates in the vicinity of the micronucleus. The boundary layer is distinct. The rectum begins from the left side of the postero-ventral surface of the endoplasmic sac and terminates in the anal opening at the base of the left ventral lobe.

Macronucleus club-shaped with a broad anterior part. Its dorsal surface is closely applied to the body wall. The anterior end of the macronucleus nearly reaches the bottom of the outer adoral furrow. The length of the macronucleus is variable, but usually it does not exceed the dorso-ventral diameter. The ellipsoidal micronucleus is situated near the boundary between the middle and anterior third of the macronucleus to the left of the sagittal plane.

The contractile vacuole is situated near the middle line of the left lateral surface ventrally to the anterior end of the left lateral groove. The centre of the vacuole in side-view is always projected ventrally to the anterior part of the oesophagus. The food consists of chloroplasts, starch granules, plant debris, yeasts and bacteria.

In Table I the results of measurements of 100 specimens of *E. rectangulatum* forma *caudatum*, taken at random from the faunule of the rumen of sheep 48, are summarized. The specimens measured were stained with Mayer's acid haemalum and mounted in Canada balsam.

Occurrence: This form was found in 54 out of 59 sheep and in 57 out of 68 Jamnapari goats examined. It comprized 3 to 10.5 per cent of the total number of *Entodinium* and from 1.9 to 7.5 per cent of the total infusorial population. It is rare in faunules from *Bos indicus* and *Bubalus bubalus*, and, if present in these, comprises less than 1 per cent of their infusorial population.

Relationship: *E. rectangulatum* f. *caudatum* is similar in the development of its caudal spination to *E. caudatum* Stein 1859, *E. acutonucleatum* Kofoid and MacLennan 1930, and *E.*

ovoidonucleatum Das Gupta 1935. (This last "species" is probably an exconjugant of *E. caudatum*.) *E. rectangulatum* f. *caudatum* differs from all these species in the position of its contractile vacuole. The lateral position of this vacuole in the new form of *Entodinium rectangulatum* is its constant character. We have not seen individuals of this form with the vacuole situated near the nucleus. Such a position is hardly thinkable, because in such a case the contractile vacuole would be situated at the bottom of the left lateral groove. Thus the new form resembles both hitherto known species of the "*laterale*" group of *Entodinium* -- *E. laterale* and *E. rectangulatum*--in the position of its contractile vacuole. The dimensions of *E. rectangulatum* f. *caudatum* nearly coincide with those of the typical form, with the exception of the length of the dorsal spine, which is much longer in the new form: 35 (26-44)µ as compared to 6 (4-8)µ in the typical form (see Table II). Slight difference in the body length may be correlated to the development of the caudal spination; it is well known, that the grade of development of this spination is inversely correlated with the body length. It is remarkable that in our material we have been unable to find the typical short-spined form of *E. rectangulatum*. The length of the dorsal spine of the new form is extreme -- it averages 101.2 per cent of the body length (see Table I), the corresponding figures for the races "A" and "B" of *Entodinium caudatum*,

TABLE II

Comparison of dimensions in μ of E. rectangulatum Kofoid and MacLennan 1930 and E. rectangulatum f. caudatum f. nova.

	E. rectangulatum after Kofoid & MacLennan	E. rectangulatum f. caudatum
Body length	35 (29-45)	35 (23-47)
Relative length	1.26 (1.1-1.5)	1.16 (0.9-1.5)
Dorso-ventral diameter	28 (23-35)	29 (23-39)
Length of macronucleus	22 (14-30)	21 (11-31)
Diameter of oral disc	15 (12-19)	17 (10-24)
Length of dorsal spine	6 (4-8)	35 (26-44)

described by Poljansky and Strelkow (1938), being 83.5 and 53.5 per cent of the body length respectively.

The morphological similarity between E. rectangulatum and E. caudatum compells one to expect that the variability of these two species will also be similar. We were prepared to find in E. rectangulatum a polymorphism, expressed mainly in the high continuous variability of development of the caudal spination. And indeed, in the faunule of the sheep 48 we found numerous forms of Entodinium of the "loboso-spinosum" type with the lateral position of the contractile vacuole similar to that of E. rectangulatum. But there were no transitional forms between the Entodinium of the "loboso-

spinosum" type and the *E. rectangulatum* f. *caudatum* -- the variation was discontinuous. Moreover, the *Entodinium* of the "*loboso-spinosum*" type were numerous, while in the populations of *E. caudatum* the "*loboso-spinosum*" forms are usually scarce. The *Entodinium* of the "*loboso-spinosum*" type, found in the faunule of the sheep 48 as well as in other sheep, was extremely similar to *Entodinium loboso-spinosum* Dogiel. As in Dogiel's description of this species (Dogiel 1925, 1927) the position of the contractile vacuole was not mentioned, it is impossible to decide whether the *Entodinium* of the "*loboso-spinosum*" type found by us is identical to, or different from, Dogiel's species. Therefore we shall discuss our form under the name *E.* cf. *loboso-spinosum* Dogiel 1927.

5. E. cf. loboso-spinosum Dogiel 1927*

(Figs. 3 - 6)

Diagnosis: Body rectangular in side-view, 26 (18-33)µ long. Contractile vacuole on the middle line of the left side of the body on the level of the micronucleus ventrally to the broad left lateral groove. One ventral lobe and one dorsal spine. Dorsal spine long with laterally flattened basis and a narrow, long distal part. Left ventral lobe fleshy and rounded. In big specimens this lobe is roughly triangular in side-view and covers the anus from the left side. In small specimens it is small, rounded and does not cover the anus. Right ventral lobe absent. The measurements given in Table III are based on 100 specimens from the faunule of sheep 48. The ciliates were stained with Mayer's acid haemalum and mounted in Canada balsam.

Description: Body nearly rectangular in side-view, 1.3 (1.1-1.7) dorso-ventral diameters in length. Oral area set nearly at right angles to the body axis. Ventral surface nearly flat, dorsal slightly convex, more so in its posterior part. Posterior end truncated nearly at right angles.

The base of the dorsal spine set in sagittal plane, laterally compressed and plough-shaped. Its distal part

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* E. loboso-spinosum was described by Dogiel in 1925 as a form of E. dubardi under the name E. dubardi forma loboso-spinosum and promoted by him to the rank of species in 1927.

produced in a long, narrow, flexible spine. Dorsal spine usually shorter than the dorso-ventral diameter. Left ventral lobe fleshy, with a rounded apex. Its size is variable: in small specimens it is relatively shorter than in big. Right ventral lobe absent.

Left lateral groove is a triangle with its apex situated between the micronucleus and the contractile vacuole near the base of the outer adoral lip. Its ventral and dorsal boundaries are less prominent than in *E. rectangulatum* f. *caudatum*. The base of the triangular left lateral groove -- i.e. the line connecting its ventral and dorsal edge on the level of the anus -- is about half the length of the dorso-ventral diameter.

TABLE III

Dimensions in μ of *E.* cf. *loboso-spinosum*, based on measurements of 100 specimens mounted in Canada balsam, from the rumen of sheep 48.

	M ± m	σ	V(%)	Observed limits of variation
Body length	26.40±0.34	±3.39	12.84	18-33
Dorso-ventral diameter	19.68±0.22	±2.24	11.32	13-25
Relative length	1.34±0.01	±0.11	8.21	1.1-1.7
Length of macronucleus	13.32±0.25	±2.53	19.00	6-20
Diameter of oral disc	10.93±0.16	±1.62	14.86	6-15
Length of dorsal spine	16.39±0.20	±2.05	12.40	12-22
Length of ventral lobe	3.53±0.12	±1.18	33.14	0.7-7.0

The mouth, the endoplasmic sack and the rectum are similar to those of *E. rectangulatum* f. *caudatum*.

The macronucleus is club-shaped, with a broad anterior part, nearly triangular in side-view. It is closely applied to the dorsal body-wall and nearly reaches the outer adoral furrow with its anterior end. Its length usually does not exceed the dorso-ventral diameter. The ellipsoidal micronucleus is situated near the boundary between the anterior and middle third of the macronucleus to the left of the sagittal plane.

The contractile vacuole is situated near the middle of the left body-surface ventrally to the left lateral groove on the level of the micronucleus. Although its position varies slightly, it never transgresses the ventral edge of the left lateral groove.

The food consists of bacteria and yeasts. The results of measurements of 100 specimens of *E.* cf. *loboso-spinosum* from the faunule of the rumen of sheep 48 are summarized in Table III. The stained specimens measured were mounted in Canada balsam. Their dimensions closely resemble those of *E. laterale* Kofoid and MacLennan 1930 as Table IV shows.

Relationship: *Entodinium* cf. *loboso-spinosum* closely resembles *E. loboso-spinosum* Dogiel, but differs slightly from it in its size and proportions (see Table V).

The outline of *E.* cf. *loboso-spinosum* is similar

TABLE IV

Comparison of dimensions in µ of E. cf. loboso-spinosum Dogiel 1927 and E. laterale Kofoid and MacLennan 1930.

	E. laterale	E. cf. loboso-spinosum
Body length	25 (19-28)	26 (18-33)
Relative length	1.28 (1.5-1.55)	1.34 (1.1-1.7)
Dorso-ventral diameter	19 (18-21)	20 (13-25)
Length of macronucleus	13 (8-18)	13 (6-20)
Diameter of oral disc	11 (9-14)	11 (6-15)

TABLE V

Comparison of dimensions of E. cf. loboso-spinosum and E. loboso-spinosum Dogiel 1927.

Species	Length	Relative length
Entodinium cf. loboso-spinosum Dogiel 1925	26 (18-33)	1.34 (1.1-1.7)
E. loboso-spinosum Dogiel 1925 from Bubalus cokei (After Dogiel)	33 (30-35)	1.57
E. loboso-spinosum Dogiel 1925, from cattle (After Dogiel)	39 (30-46)	1.50

to that of E. loboso-spinosum, depicted by Dogiel (1927, Fig. 27a, p. 60)(see p. 7 of the present paper).

Dogiel states that both ventral and dorsal surfaces of E. loboso-spinosum are convex, but Figure 27"a" of his monograph, in which E. loboso-spinosum is depicted, shows an

Entodinium with a nearly flat ventral surface closely resembling in its outline *E.* cf. *loboso-spinosum*. The differences in dimensions and proportions of *E.* cf. *loboso-spinosum* and *E. loboso-spinosum* Dogiel probably lie within the limits of individual variation. The position of the contractile vacuole in "*E. dubardi* f. *loboso-spinosum*", described by Dogiel in 1925, is not mentioned in this description, nor is it in his monograph of 1927, in which this "forma" has received the rank of a species. Therefore it is impossible both to differentiate or to identify *E.* cf. *loboso-spinosum* with Dogiel's *E. loboso-spinosum* without a re-examination of the type-specimens of the latter species.

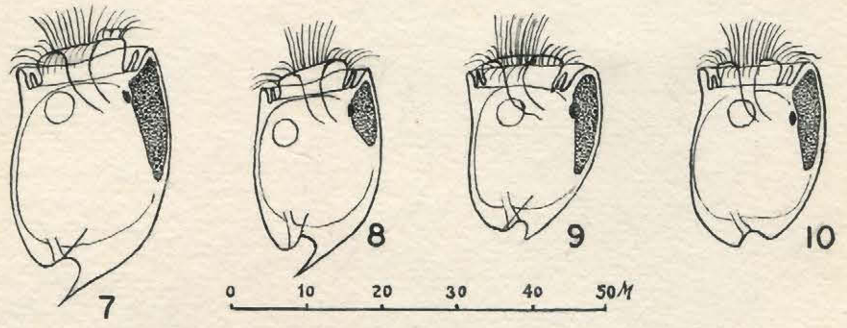
Occurrence: *E.* cf. *loboso-spinosum* was present in 42 out of 57 goats and in 36 out of 54 sheep examined.

6. The "*dubardi*" forms of *E.* cf. *loboso-spinosum*.

Tailless forms of *E.* cf. *loboso-spinosum* were not found in the faunule of sheep 48 but were present in other faunules of both sheep and goats. Of these the faunule of the Jamnapari goat G59 was of special interest. In this faunule *E.* cf. *loboso-spinosum* was the sole species of *Entodinium* with the lateral position of the contractile vacuole. The range of variability of its caudal spination embraced short-tailed typical forms on the one hand and tailless forms of the "*dubardi*" type on the other, with a continuous series of intermediary variants between them (Figs. 7-10).

The position of the contractile vacuole in these forms varied slightly: whereas in some specimens this vacuole was situated near the ventral margin of the oesophagus (Figs. 9 and 10), in others it was shifted further ventrad, being situated in some individuals half way between the level of the oesophagus and the ventral side of the body (Figs. 7 and 8). In these last forms the position of the contractile vacuole was similar to that in *E. caudatum* depicted by Schuberg (1888).

The left lateral groove was present in the spinose forms but became progressively shallower as the length of the caudal spination decreased, and was not discernible in the tailless forms of the "*dubardi*" type.



Figs. 7 to 10 -- *E.* cf. *loboso-spinosum* from the faunule of the goat 59.

Note the variability of the caudal spination and the position of the contractile vacuole ventrally to the level of the oesophagus.

7. Entodinium simulans sp. n., forma caudatum f. nova

(Figs. 11, 12, 17)

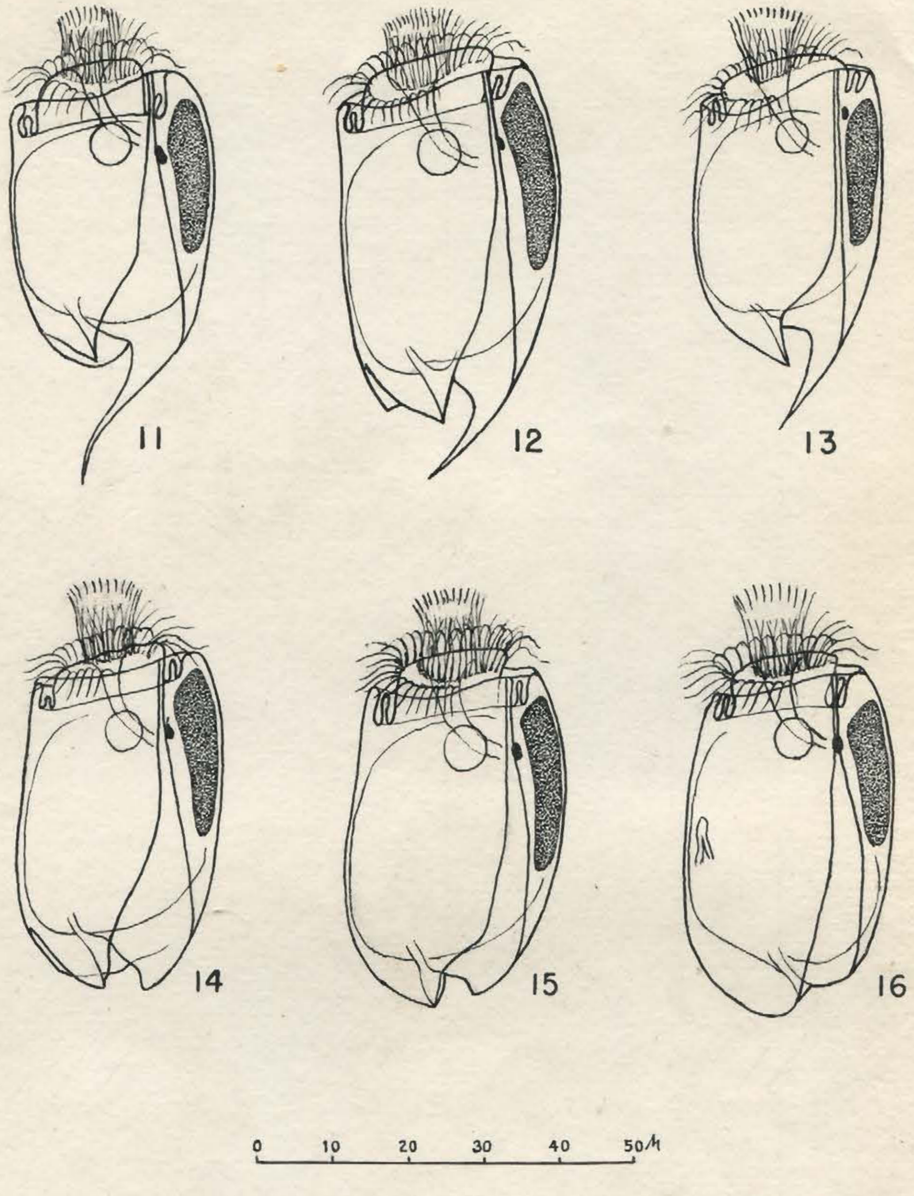
Diagnosis: Body ovoidal in side-view, 35 (27-44)µ long and 28 (21-34)µ deep. Contractile vacuole on the middle line of the left side of the body on the level of the micronucleus ventrally to the left lateral groove. Left lateral groove narrow, long, slit-shaped in its anterior half. Its anterior end extends to the distal margin of the outer adoral lip. Oral disc slanted to the left. Outer adoral lip very low in its left ventral part. Two ventral lobes and one dorsal spine. Dorsal spine much shorter than the dorso-ventral diameter. Left ventral lobe fleshy, triangular, with the anal opening at its base. Right ventral lobe rounded with an acute apex. The description and the measurements compiled in Table VI are based on 100 stained and mounted specimens from the rumen of sheep 54.

Type host: domestic sheep.

Type locality: Rawalpindi, W. Pakistan. Collected in June 1951.

Type specimens are preserved in the Institute of Parasitology, Macdonald College, Province of Quebec, Canada.

Description: Body ovoidal in side-view, 1.28 (1.0-1.5) dorso-ventral diameters in length. Oral disc in side-view set nearly at right angles to the main body axis, but slanted to the left so that the free base of the outer



Figs. 11 to 18 -- E. simulans sp. n. from the faunule of the sheep 54.

Figs. 11 and 12 -- the "caudatum" type; Fig. 13 -- the "loboso-spinosum" type; Figs. 14 to 16 -- spineless forms with varying degrees of development of the caudal lobes.

adoral cilia lies on the level of the bottom of the outer adoral furrow. Outer adoral lip very low in its left anterior part. The apex of the left lateral groove extends as a narrow furrow to the anterior edge of the outer adoral lip. Posterior end of the body slightly tapered, ventral lobes being directed postero-dorsally.

Dorsal spine much shorter than the dorso-ventral diameter. The base of this spine is set in sagittal plane, laterally compressed and plough-shaped. Its distal part produced in a narrow flexible spine. Left ventral lobe fleshy, triangular, slanted dorsally at an angle of about 30-40°. The anal opening situated at the base of the left ventral lobe and continuing as a shallow furrow running in the direction of the apex of this lobe. Right ventral lobe rounded, with an acute apex. Left lateral groove narrow and long; its width at the level of the anus less than half the dorso-ventral diameter. At the level of the micronucleus the left lateral groove tapers to a narrow furrow, reaching the anterior end of the outer adoral lip.

The mouth is an ellipsoidal opening slanted to the left. The oesophagus situated to the right from the anterior pole of the endoplasmic sac. It is bent dorsad and terminates in the vicinity of the micronucleus. The boundary layer is very distinct. The dark-stained endoplasm contrasts with the very light-stained ectoplasm. The rectum begins from the left side of the posteroventral surface of the endoplasmic sac and terminates in the anal opening at the base of the left ventral lobe. Macronucleus club-shaped with a broad anterior end, nearly triangular in side-view. It is closely applied to the dorsal body-wall and reaches the outer adoral furrow. The ellipsoidal micronucleus is situated near the boundary between the anterior and middle thirds of the macronucleus.

The contractile vacuole is situated at the level of the micronucleus ventrally to the left lateral groove. In left side-view it is projected on the anterior part of the oesophagus and the antbrior pole of the endoplasmic sac.

The food consists of bacteria and yeasts. Spores of fungi and fragments of micelium, as well as starch granules have been occasionally seen in the endoplasmic sac.

Measurements, summarized in Table VI, were taken from 100 stained and mounted specimens of *E. simulans* sp. n. from the rumen of sheep 54.

Occurrence: *E. simulans* was found in the faunules of 30 out of 59 sheep and 33 out of 57 Jamnapari goats examined.

Relationship: In its caudal spination and the position of the contractile vacuole *E. simulans* is similar to *E. laterale* and *E. rectangulatum* described by Kofoid and MacLennan in 1930. It differs from both these species in having a very long and narrow slit-shaped left lateral groove. The extension of this groove on the outer adoral lip is a peculiarity not described in any other species of *Entodinium*.

It has to be noted that *E. simulans* exhibited in the faunule of sheep 54, as well as in other faunules, a continuous variation in the development of the caudal spination, similar to that of *E. caudatum*. Two forms, connected by transitional variants, could be distinguished -- the *E. simulans* f. *loboso-spinosum* and *E. simulans* f. *dubardi*; these forms are described below.

TABLE VI

E. simulans sp. n., f. *caudatum* f. nova

Summary of measurements (in µ) of 100 specimens, stained and mounted in Canada balsam.

	M ± m	σ	V(%)	Observed limits of variation
Body length	35.47±0.38	±3.82	11.07	27-44
Dorso-ventral diameter	27.62±0.28	±2.80	10.14	21-34
Relative length	1.28±0.01	±0.10	7.81	1.0-1.5
Length of macronucleus	22.57±0.30	±3.00	13.29	16-29
Diameter of oral disc	14.85±0.15	±1.49	10.04	10-18
Length of dorsal spine	17.05±0.35	±3.52	20.64	10-27
Length of left ventral lobe	6.86±0.11	±1.12	16.33	2-10
Length of right ventral lobe	6.65±0.13	±1.29	19.40	3-10

8. E. simulans sp. n.,
forma loboso-spinosum, forma n.
(Figs. 12, 13)

Diagnosis: Similar to E. simulans f. caudatum, except in the development of the right ventral lobe which is absent or reduced to a narrow cuticular fold without pointed end. The left ventral lobe may be pointed, as in the "caudatum" form, or rounded. This form was very rare in the faunule of sheep 54. The measurements, recorded in Table VII, are based on seven specimens from this faunule.

TABLE VII

E. simulans sp. n. forma loboso-spinosum f. nova

Summary of measurements (in μ) of 7 specimens, stained and mounted in Canada balsam, from the faunule of sheep 54.

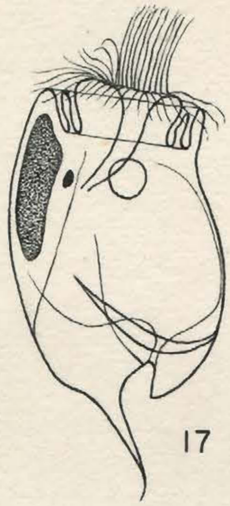
	Observed mean and limits of variation
Length	38 (25-46)
Dorso-ventral diameter	27 (22-34)
Relative length	1.36 (1.10-1.50)
Length of macronucleus	17 (12-23)
Diameter of oral disc	14 (11-16)
Length of dorsal spine	14 (10-17)
Length of ventral lobe	7 (6 - 9)

9. *E. simulans* sp. n., forma *dubardi*, forma n.

(Figs. 16, 18)

Diagnosis: Similar to *E. simulans* f. *caudatum* and *E. simulans* f. *loboso-spinosum* except in the development of the caudal armature. Spines absent, right ventral lobe absent. Left ventral lobe and caudal lobe short, rounded, without pointed angles. Left lateral groove as in *E. simulans* f. *caudatum*, but sometimes shallow. Contractile vacuole always near the middle line of the left body side at a considerable distance from the nuclear apparatus. Measurements, summarized in Table VIII, are those of 100 stained specimens, mounted in Canada balsam, from the faunule of sheep 54.

E. simulans forma *dubardi* is a tailless form of *E. simulans* sp. n., analogous to forms of *E. caudatum*, designated by Poljansky and Strelkow (1934, 1938) as "*simplex*". The grounds for designating these forms as "*dubardi*" forms were briefly stated in the chapter on materials and methods. Their further discussion necessitates an inquiry into the validity of Dogiel's species *E. simplex*.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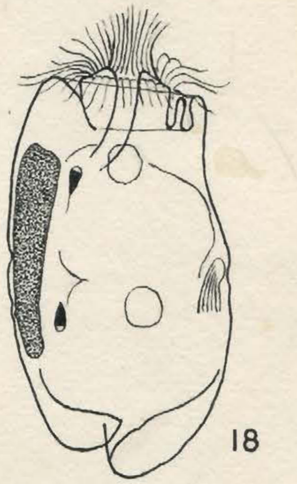
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Fig. 17 -- E. simulans sp. n. forma caudatum with a reduced right ventral lobe. Right-side view.

Fig. 18 -- E. simulans sp. n. forma dubardi. Right-side view of a dividing specimen.

TABLE VIII

Dimensions (in μ) of *E. simulans* f. *dubardi* from the rumen of sheep 54, based on measurements of 100 specimens, stained and mounted in Canada balsam.

	M ± m	σ	V(%)	Observed limits of variation
Length	31.92±0.57	±5.72	14.60	21 - 47
Dorso-ventral diameter	23.04±0.35	±3.46	15.04	16 - 34
Relative length	1.37±0.01	±0.11	8.02	1.2 - 1.7
Length of macronucleus	17.87±0.36	±3.61	20.11	11 - 28
Diameter of oral disc	12.26±0.24	±2.42	19.66	8 - 20
Length of dorsal lobe	3.52±0.12	±1.21	34.38	1.3 - 8.6
Length of ventral lobe	6.05±0.12	±1.22	20.18	2.7 - 10.0

10. E. simplex Dogiel 1925 -- a synonym of E. dubardi Buisson 1923.

Dogiel has described E. simplex in 1925 and given, as the sole character distinguishing this species from E. dubardi, its relative length, which in Dogiel's species is 1.7-1.74, whereas in E. dubardi it is 1.55 (see Dogiel, 1927). However, the relation of width to length of 1.7-1.74 is not in agreement with Dogiel's drawings of E. simplex accompanying the description of this species (see Dogiel 1925b, p. 45, Fig. 2 and Dogiel 1927, p. 41, Figs. 3 and 4). Our measurements of these figures have shown that the length to width relation of the depicted specimens varies from 1.50 to 1.68 with the average of 1.62, which is very close to the length to width relation of 1.55 characteristic, according to Dogiel, of E. dubardi Buisson 1923. As the relative length is the sole character distinguishing E. simplex Dogiel 1925 from E. dubardi Buisson 1923, it has to be stated that the former species is a synonym of the latter.

Eleven years after the publication of Dogiel's monograph on Ophryoscolecidae (1927), his pupils -- Poljansky and Strelkow -- described a strain of what they call "E. simplex Dogiel" (see pp. 72-77 of their paper of 1938). The variability of dimensions of "E. simplex" of their clone is summarized by them in a table (see l.c., table 36, p. 73), in which, however, at variance with Dogiel's monograph, the inverse relation -- that of width to length -- is given. Our recalculations of this table have given the following results: on September 11, 1934 the average length-to-width relation of E. simplex was 1.25 with limits of variation of 1.06 to 1.56; on October 23, 1934, the average was 1.47 with limits of variation from 1.28 to 1.67, and on December 23, 1934 the corresponding figures were 1.35 with limits of 1.04 and 1.64. It is hard to conceive why a strain of Entodinium with such characteristics should be identified as E. simplex. Poljansky and Strelkow's illustrations are in full agreement with figures given by them in their tables. On measuring 10 specimens of "E. simplex" depicted by these authors in their Figure 23A (l.c., p. 75) we found the length to width relations to be 1.45 with limits of variation of 1.33 to 1.53, the corresponding figures for their Figure 23B being 1.55 (1.39 to 1.70), which is very close to the figures characteristic, according to Dogiel's monograph, of E. dubardi.

Describing the "simplex" forms of E. caudatum Poljansky and Strelkow state that "quand Ent. caudatum est a l'état de "simplex" son phenotype ne diffère en rien de celui du vrai Ent. simplex."(l.c., p. 74). The corresponding figures (l.c., Fig. 25, p. 76) represent 10 specimens of the "Ent. caudatum a l'état "simplex"" with the average length to width relation of 1.52 with variations from 1.43 to 1.60 -- again figures characteristic, according to Dogiel's monograph, of *E. dubardi*. Hence it follows, that the "vrai *Ent. simplex*" of Poljansky and Strelkow is identical to *E. dubardi* Buisson 1923, and that the tailless forms of their class VI of *E. caudatum* are phenocopies of *E. dubardi*, not of "*E. simplex*".

In their paper of 1938 Poljansky and Strelkow state that the variants of class VI are similar to both *E. simplex* and *E. dubardi*, but that "*Ent. dubardi* forma *dubardi* trouvé dans *Capreolus capreolus*, *Cervus canadensis* et les Antilopes d'Afrique, vue la difference de l'hôte, convient moin pour la comparaison" (l.c., p. 20). Why this argument -- the difference of hosts -- should not be applicable to *E. simplex*, described by Dogiel from the reindeer (1925b), is hard to understand.

As *E. simplex* Dogiel 1925 is a synonym of *E. dubardi* Buisson 1923, we have designated the tailless forms of *E. simulans* sp. n. as forms of the "*dubardi*" type. This designation is the more appropriate as the relative length of these forms is close to that of *E. dubardi*.

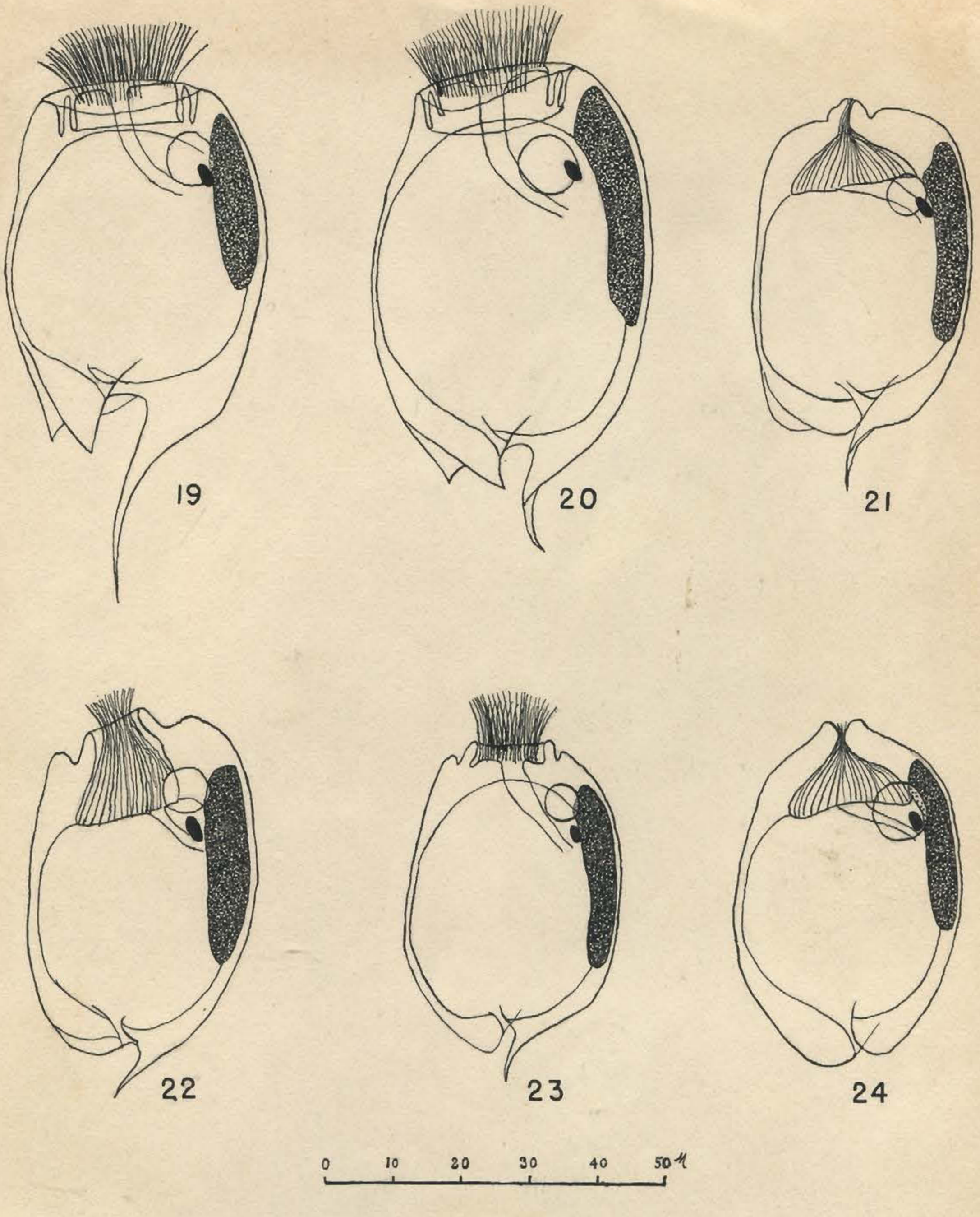
11. E. caudatum Stein 1859

E. caudatum Stein 1859 *sensu* Dogiel 1927 is similar to the above described species of *Entodinium*, but differs from them by its more rounded body, larger size, shorter left lateral groove, and, before all -- in the position of its contractile vacuole which in this species is adjacent to the macronucleus. This species was found by us only once -- in the sheep N2 from Rawalpindi (see Figs. 19-24).

The faunule of this sheep consisted of only 4 species of Ophryoscolecidae and of one of Isotrichidae. The numerical interrelations between individuals belonging to these species were as follows:

E. caudatum	93.0%
E. longinucleatum	2.5%
E. ovinum	2.5%
Polyplastron multivesiculatum	+
Isotricha prostoma	2.0%

E. caudatum was represented by all 6 classes of development of the caudal spination, the continuous character of variation being obvious from first sight. The distribution of individuals among the classes was as follows:



Figs. 19 to 24 -- E. caudatum Stein 1859 from the rumen of sheep 2. Specimens of the I-VI classes.

TABLE IX

Distribution of individuals of *E. caudatum* among the classes of development of the caudal spination. (Material from sheep 2)

Classes	I	II	III	IV	V	VI
Per cent individuals	9.0	4.5	1.5	0.5	4.0	80.5

The character of distribution was thus similar to that observed by Poljansky and Strelkow in their clones of *E. caudatum*. The fourth class -- that of individuals with the caudal spination of the *loboso-spinosum* type -- was represented by a few individuals only. The body-length in all classes varied from 28 to 65μ, but that of the tailed classes (I-V) -- only from 38 to 65μ. The tailed individuals were thus on the average slightly larger than the tailless forms. The relation of length to width varied from 1.1 to 1.7 with the average of 1.37 ± 0.01. This relation in individuals of the 6th (tailless) class alone was 1.39 ± 0.01. The relation was thus closer to that of *E. dubardi* (1.55) than to that of Dogiel's "*E. simplex*" (1.70) -- as the case was in clones examined by Poljansky and Strelkow. The limits of variations of the relative length in the population of sheep 2 was also comparable to that observed in clones of *E. caudatum*, studied by these authors.

12. Discussion

The species of *Entodinium*, described in the foregoing pages, are related to both *E. caudatum* Stein *sensu* Dogiel 1927 and *E. caudatum* Stein *sensu* Schuberg 1888, and exhibit an intraspecific variability, both continuous and discontinuous, producing series of forms, similar in the structure of their caudal spination to those of the forms of *E. caudatum*, described by Poljansky and Strelkow (1934, 1938). Our material -- fixed faunules -- is unsuitable for an experimental analysis of the nature of this variability. However, with considerable degree of probability we can presume that both environmental and genetic factors participate in its production.

Due to the parallel variation of the caudal spination in *E. caudatum* on the one hand and in *E. rectangulatum* and *E. simulans* on the other, three different forms of the "*caudatum*" and the "*loboso-spinosum*" types were present in our material (see Figs. 26, 27, 29, 30, 32, 33). An attempt to identify these forms with the aid of the existing keys -- that of Dogiel (1927) and of Bhatia (1936) -- the last being based on the first -- would have lead to the discouraging result of being forced to identify three obviously different forms with the "*caudatum*" type of the caudal spination as *E. caudatum*, and three corresponding forms with the "*loboso-spinosum*" type of spination -- as *E. loboso-spinosum*. Such result depends on the principle, on which Dogiel's key was built -- i.e. on an attempt to define species of Entodinium as well as of the higher Ophryoscolecidae whenever possible on the basis of the character of their caudal spination. This usage was started by Stein in 1859 and perpetuated by all subsequent students of these ciliates, including Kofoid. The use of the structure of body-appendages in the systematics of the Ophryoscolecidae seemed to be simple, convenient in practice, and, as far as could have been judged by analogy with other groups of animals, reasonably reliable. Zoology has originated basically on the foundation of studies on vertebrates and higher arthropods, and the practice has shown that the structure of body-appendages in these groups is constant and therefore of considerable taxonomic value. It is natural that this practice was extended into the realm of zoology of lower animals, in which, however, it proved to be of limited value. Thus, e.g., the experimental study of temporal variation in Cladocera has shown that many morphological characters of this group, believed by early systematists to be of taxonomic value, as e.g., the length of helmet, of the rostrum and of the caudal spine, were environmentally variable, the intraspecific variability producing forms once believed to be good species and even to belong to different genera (Daphnia and Hyalodaphnia)(see Coker and Addlestine, 1948). Numerous species of Daphnia, Bosmina and of some other genera have had to be suppressed. An analysis of environmental factors involved was started by Wesenberg-Lund (1900-1910), who found that seasonal changes of water temperature are the most important factor. Later Woltereck (1909-1921 and 1934) showed that the leading factor is the level of nutrition, associated with seasonal changes of the temperature.

Recent investigations confirmed the participation of both temperature and nutrition in the causation of cyclomorphosis, but showed also that other factors, as e.g., turbulence of water (Brooks, 1947), participate in its production. However, the capacity to cyclomorphosis, the norm of reaction, is determined genetically. Within one species may exist several races differing in the degree and character of their morphogenetic responses to environmental factors.

Another example of confusion in systematics caused by pronounced environmental and genetical intraspecific variability is the well known history of examination of the brine-shrimp <u>Artemia salina</u>. Forms of this species, arising under the influence of salinity-changes were thought at the end of the last century to be good species, and some of them -- even to belong to a different genus (Schmankewitsch 1875). Experimental analysis of this variability has shown that both environmental and genetic factors participate in its causation (Gross 1932). Similar examples can be drawn from the systematics of molluscs (e.g. <u>Ostrea</u>, <u>Mytilis</u>, <u>Vermetus</u>, *Anodonta*, and other genera) as well as from that of annelids, Bryozoa, and Rotatoria (*Keratella*, *Brachionus* *et* *al*.) (Wundsch 1921, and others). In all cases where a careful analysis of the nature of the variability was attempted, it was shown to be produced by interaction of environmental and genetic factors.

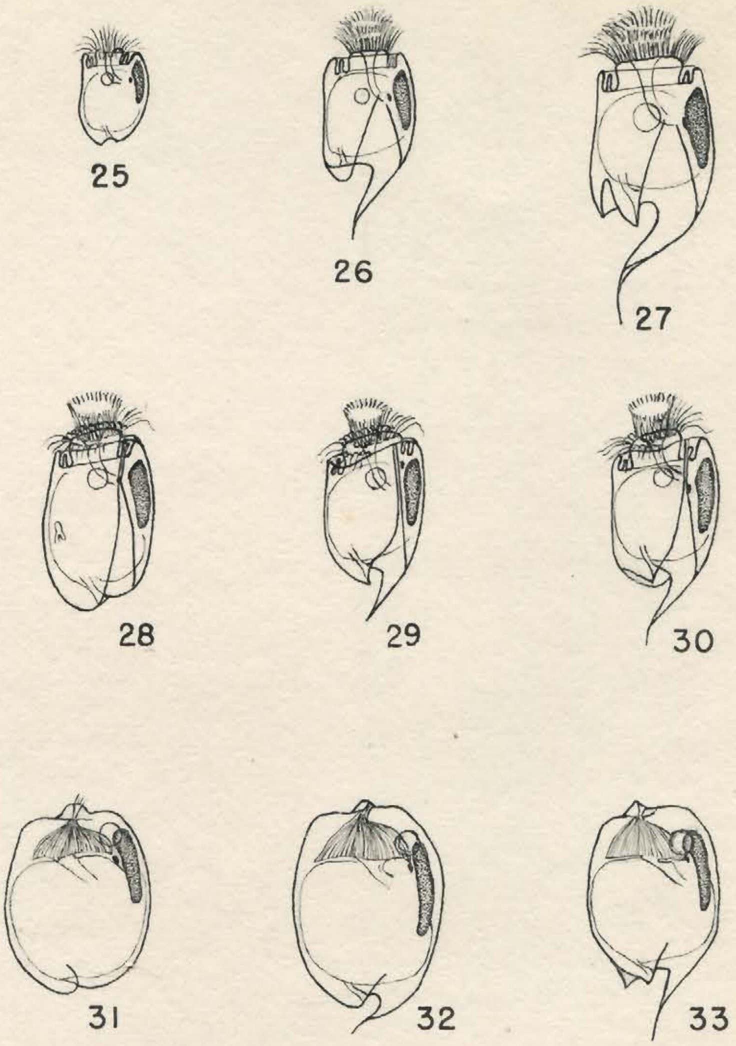
A similar type of variability in the fresh-water dinoflagellates was described by Wesenberg-Lund as early as 1908. Later Kofoid reported the presence in chain-forming species of *Ceratium* of what he calls mutations, but what may well be modifications, affecting traits, usually evaluated as species-characters.

The systematics of Ophryoscolecidae are at the present time in a state comparable to that of the systematics of Cladocera and Dinoflagellata at the time when the basic concepts of the doctrine of cyclomorphosis have been evolved, i.e. half a century ago. The diagnoses of many species of the Ophryoscolecidae, and specially of those possessing caudal armature, are based on intraspecifically variable characters, and therefore forms belonging to one species are often split into several "species". This is the case not only within the "*caudatum-laterale*" group of *Entodinium* but also in some species of other genera of this family. Poljansky and Strelkow have shown, e.g. that forms of *Eudiplodinium*, described by Dogiel as *E. neglectum* f. *dilobum*, *E. neglectum* f. *monolobum* and *E. neglectum* f. *bovis*, and promoted to the rank of species by Kofoid and MacLennan in 1932 are environmentally induced modifications of one species, and not separate species, as Kofoid and MacLennan presumed. On the other hand it is nearly certain, that some other forms of *Eudiplodinium neglectum*, described by Dogiel, as e.g. *E. neglectum* f. *insigne*, *E. neglectum giganteum*, which also were promoted by Kofoid and MacLennan to the rank of species, really are good species. Poljansky and Strelkow have shown that, whereas some species of the Ophryoscolecidae are extremely environmentally plastic (e.g. *Entodinium caudatum*, *Eudiplodinium neglectum* f. *dilobum*), others, as e.g. *Eudiplodinium maggii*, *Entodinium vorax*) are stable. Woltereck, who observed similar phenomena in Cladocera, has divided species, examined by him, into the groups of stenotypic species with a low grade of intraspecific variability and of schizotypic species with high intraspecific variability -- terms which roughly correspond to labile and stable species of Schmalhausen (1949). In these terms the basic difficulty of the systematics of the Ophryoscolecidae can be defined as the difficulty in dealing with morphological characters of labile species.

Another difficulty of the systematics of these ciliates lies in the presence of parallel forms in related species, which, when identified on the basis of the parallel varying characters, are lumped together into one species. A complete reconstruction of the systematics of the Ophryoscolecidae can be achieved only on the basis of an experimental analysis of variability in clones, maintained in experimental animals and in (anaerobic) cultures. A more or less complete study of the variability of their numerous species will require many decades of strenuous work. Life-time efforts of several generations of zoologists will probably be needed to conduct the systematics of the Ophryoscolecidae between the Scilla and Charybdis of environmental plasticity and of parallel variation to the safety of exact knowledge, based on experimental data.

However, a mitigation of vices of the present-day systematics of the Ophryoscolecidae can be achieved by careful selection of characters used for identification of its species. Strict distinction should be made, whenever possible, between intraspecifically variable characters ("Gestaltmerkmale" of Woltereck), and stable characters of taxonomic value ("Taxonomische Merkmale" of Woltereck) -- a distinction which to a certain degree coincides with Vavilow's (1923) distinction between varietal characters and characters belonging to "radicals" of Linneons.

Such distinction is of special importance in systematics of groups with parallel variation, due to possibility of confusion between intraspecific and inter-specific parallel variation. The intraspecific variability often affects prominent characters, which sometimes can be mistaken for specific characters.



Figs. 25 to 33 -- Parallel forms of *Entodinium* of the "*caudatum-laterale*" group. Left column -- the "*dubardi*" types, middle column -- the "*loboso-spinosum*" types, right column -- the "*caudatum*" types.

Fig. 25 -- The "*dubardi*" and Fig. 26 -- the "*loboso-spinosum*" form of *E.* cf. *loboso-spinosum* Dogiel 1927.
Fig. 27 -- *E. rectangulatum* Kofoid and MacLennan 1930 f. *caudatum* f. n.
Fig. 28 -- *E. simulans* sp. n. f. *dubardi* f. n.
Fig. 29 -- *E. s.* sp. n. f. *loboso-spinosum* f. n.
Fig. 30 -- *E. s.* sp. n. f. *caudatum* f. n.
Fig. 31 -- *E. caudatum* Stein 1859 *f. dubardi*.
Fig. 32 -- *E. caudatum* f. *loboso-spinosum*.
Fig. 33 -- *E. caudatum* f. *caudatum*.

This source of errors exists both in zoological and botanical systematics, and becomes of considerable importance in cases of discontinuous intraspecific variability. "Varietal alternative characters," says Vavilow (1923) "were often mixed with those of radicals; particularly was this the case when descriptions of new genera and Linneons were made on single plants and samples collected in one district."

Awerinzew and Mutafova (1914) who were the first to draw the attention to the parallelism of forms in Ophryoscolecidae, wrote, that these ciliates "... in Reihen angeordnet werden können, die den Reihen eines eigenartigen periodischen Systems entsprechen, so dass vermittels einer besonderen Tabelle die Formen erraten werden können, die zunächst weder gefunden noch beschrieben, wie es unsere Befunde teilweise zeigen, jedoch vorhanden sind und später aufgefunden werden können." In this wording the term "species" in not used. Tables, illustrating parallelism of forms in the Ophryoscolecidae, were published in 1923 by Crawley and by Dogiel. Crawley, discussing taxonomic characters of the Ophryoscolecidae, states that "In the case of the Ophryoscolecidae, as has been pointed out, the generic characters are those which have to do with the cirrus system, the specific being the size and the nature of the armature". Thus environmentally plastic characters were proclaimed by Crawley to be specific characters. In a paper published simultaneously with that of Crawley, Dogiel (1923) says: "Meistens ist die Zahl der Dornen in jeder

Art streng konstant, doch gibt es Arten, wo diese Konstanz in sältenen Fällen verloren geht, und auch andere, wo im Bereiche der Art mehrere "Formen" mit verschiedener Zahl der Dornen entstanden sind (O. fasciculus mit 6 verschiedenen "Formen", die 0 bis 5 Dornen besitzen)"(l.c., p. 108). In his later papers Dogiel tended to unite series of forms into species, including in them, at least in some instances, "forms" which obviously are independent species.

The tables of Crawley and of Dogiel, illustrating the parallelism of forms in the Ophryoscolecidae, have been compiled over 30 years ago and are now out of date. The data on the intraspecific variability in this family now at hand are inadequate for a compilation of an up-to-date table. It is probable also, that a revision of some basic concepts of the comparative morphology of this family will be needed to obtain a deeper insight into the homologization of structures in the higher genera of this family with those of Entodinium.

Parallelism of forms is not an exclusive trait of the family Ophryoscolecidae, but is known to exist in other classes of Protozoa as well. Hoare (1933), studying Eimeriidea from Uganda, has shown that "When the genera comprising this suborder (with a few exceptions) are arranged in the ascending order of the number of structural elements (sporocysts and sporozoites) contained in their oöcysts, they form parallel series or groups in the horizontal and vertical directions, which consist of homologous members, as represented graphically... The oöcyst characters of each genus are determined by those of its neighbours in the horizontal and vertical groups." In the graph, given by Hoare, were left vacant places for as yet undiscovered genera with predicted structure of oöcysts. At least three genera, filling the vacant places in Hoare's graph, were described since the publication of his paper (Gouseff 1937, Ray _et al_ 1942, Vincent 1936) -- a unique case of prediction of existence of new genera in zoological literature.

Parallelism of forms in _Entodinium_ of the "_caudatum-laterale_" group, described in the present paper, is expressed in repetition of types of caudal spination in different species of this group. The "_caudatum_", _loboso-spinosum_" and "_dubardi_" types are produced by the intraspecific variability in _E. caudatum_, _E. simulans_, as well as in the group _E. rectangulatum_ plus _E._ cf. _loboso-spinosum_ (see Figs. 25 to 33). The character of variation of the caudal spination in these species is, however, different. Whereas in _E. caudatum_ and _E. simulans_ the variation is obviously continuous and the percentage of the "_loboso-spinosum_" forms extremely low, in the group _E. rectangulatum_ and _E. loboso-spinosum_ the percentage of "_loboso-spinosum_" forms is very high and the variation discontinuous. Our material is not suitable for an experimental analysis of relationships between _E. rectangulatum_ and _E._ cf. _loboso-spinosum_. Although these two forms have been found nearly always together, we have not found transitional forms between them. Two explanations of these findings are possible: 1. E. rectangulatum and E. cf. loboso-spinosum are distinct species, and 2. E. rectangulatum and E. cf. loboso-spinosum are forms belonging to one species. If this last presumption is accepted, we would have to explain the discontinuous character of variability in the species by participation of genetic factors, may be connected with polyploidy. These questions can, however, be further elucidated only by experimental methods.

The stereotyped forms of the caudal spination in the species of the "caudatum-laterale" group of Entodinium appear thus in at least three species of this group, differing from each other in essential morphologic characters -- the development and the shape of the left lateral groove and the position of the contractile vacuole. In E. caudatum the contractile vacuole is situated near the anterior end of the macronucleus, as it is in the vast majority of species of this genus. The left lateral groove in E. caudatum is less developed, than in E. rectangulatum and E. simulans. This compells us to regard E. caudatum as a primitive member of the "caudatum-laterale" group. In E. rectangulatum and E. cf. loboso-spinosum the contractile vacuole became displaced ventrad to the level of the oesophagus, and the anterior end of the elongated left lateral groove separates this vacuole from the nuclear apparatus. In E. simulans the elongation of the left lateral groove has resulted in its extension on the outer adoral lip. Simultaneously the left lateral groove became transformed in a furrow. This compells us to regard *E. simulans* as an advanced member of the "*caudatum-laterale*" group.

Thus in the "*caudatum-laterale*" group of *Entodinium* exists an evolutionary trend to ventrad displacement of the contractile vacuole and to the transformation of the left lateral groove into a long and narrow furrow, extending on the adoral lips. The probable significance of these evolutionary trends in the macro-evolution of the Ophryoscolecidae shall be discussed in the second part of this paper.

PART II

ON THE ORIGIN OF THE HIGHER OPHRYOSCOLECIDAE.

"... the idea of equivalency or proportion, as well as that of likeness, ought always to govern the labours of a classifier."

Richard Owen, Lectures on the Comparative Anatomy, 1843.

The family Ophryoscolecidae is divided into two groups: the lower Ophryoscolecidae, comprizing only one genus *Entodinium*, and the higher Ophryoscolecidae, comprizing all other genera of this family. The genus *Entodinium* is characterized by the presence of only one membranelle zone -- the adoral, of one contractile vacuole, and by the micronucleus situated ventrally to the macronucleus. Higher Ophryoscolecidae have two membranelle zones -- the adoral and the dorsal, two or more contractile vacuoles and the micronucleus situated dorsally to the macronucleus.

There is no doubt that the higher Ophryoscolecidae originated from ancestors similar to existing species of the genus *Entodinium* (Dogiel 1923, Crawley 1923). According to Dogiel, the dorsal membranelle zone of *Diplodinium* s. str. (Dogiel's subgenus *Anoplodinium* of the genus *Diplodinium* s. lato) originated as result of dorsad growth of the left outer end of the oral membranelle zone of *Entodinium* which in the course of this growth bent to the left and thus produced the semicircular adoral zone of *Diplodinium* s. str. Simultaneously the contractile vacuole and the micronucleus were displaced dorsad and thus became situated dorsally to the macronucleus. Thus Dogiel takes it for granted, that the dorsal side of higher Ophryoscolecidae is homologous to the dorsal side of *Entodinium*. In his paper on the phylogeny of Ophryoscolecidae, published in 1946, and later in his textbook of general protozoology (1951, p. 430) Dogiel depicts a hypothetical _Entodinium_, ancestral to higher Ophryoscolecidae, with its micronucleus situated dorsally to the macronucleus -- a character not observed in any existing species of this genus.

In 1923, Crawley wrote: "It is impossible to avoid the conclusion, that _Diplodinium_ (s. lato; author) is derived from _Entodinium_. What apparently has happened is that the right and the left sides of the anterior surface of _Entodinium_ have grown in, separating the originally large mouth into two portions. Of these, the larger ventral portion has continued as a functional mouth, while the smaller dorsal portion has become reduced to a pit extending but a short distance into the interior. At the same time, the original single system of cirri has also separated into two, producing one crown, which encircles the mouth and another which encircles the pit..." Dogiel (1927) correctly states, that there is no pit in the middle of the dorsal membranelle zone of _Diplodinium_ and that this zone does not form a closed spiral*. Thus the morphological characters, required by the theory of Crawley, do not exist in the genus _Diplodinium_.

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* Crawley's opinion on the existence of such a pit was probably based on the incorrect drawings of Eberlein, who has depicted such pits in _Eudiplodinium maggii_ (= _D. maggii_) and _D. dentatum_ (1895, plate 7, Figs. 8, 9 and 17) and of Awerinzew and Mutafowa, who have represented such pits in their figures of _Ostracodinium dentatum_ (their "_D. dentatum_") and _Metadinium medium_ (1914, plate 9, Figs. 1, 2 and 7).

A hypothetical reconstruction of the long series of ancestral forms, connecting typical higher Ophryoscolecidae to typical primitive species of *Entodinium*, meets with considerable difficulties. Morphological characters, which according to the views of both Crawley and Dogiel should be present in ancestral forms of higher Ophryoscolecidae, as e.g. the dorsad growth of the oral membranelle zone and the displacement of the micronucleus to the dorsal side in *Entodinium*, are not found in existing species of this primitive genus. In this paper an attempt will be made to interpret the morphology of the *lower* representatives of higher Ophryoscolecidae on the basis of evolutionary trends, observed in some *higher* representatives of the genus *Entodinium*.

One of the most primitive genera of higher Ophryoscolecidae is doubtless the genus *Diplodinium* s. str. in the sense of Kofoid and MacLennan (1932). This genus lacks a skeleton, which is characteristic of all other genera of higher Ophryoscolecidae with the exception of *Eodinium*. Another peculiarity of *Diplodinium* is the localization of the nuclear apparatus not near the dorsal side -- as is the case in all other genera of Ophryoscolecidae -- but near the middle of the right side of the body. A long narrow longitudinal furrow is situated between the nuclear apparatus and the contractile vacuoles of *Diplodinium* s. str. and *Eudiplodinium* *sensu* Kofoid and MacLennan. Any theory aiming to explain the origin of the higher Ophryoscolecidae must also explain the genesis of these peculiar traits of these two primitive genera of this group.

Studying the morphology of two species of Entodinium related to E. caudatum -- the E. rectangulatum Kofoid and MacLennan 1930 and E. simulans sp. n., we have noted that in the last two species of Entodinium exists a trend to anteriad elongation of the left lateral groove, which in E. simulans becomes transformed in a long and narrow furrow. The contractile vacuole in these species of Entodinium is shifted ventrad to the level of the mouth and becomes separated from the nuclear apparatus by the anterior portion of the elongated left lateral groove.

The comparison of interrelations of organelles on the left body-side of Entodinium simulans with those on the right body-side of Diplodinium, e.g. D. dentatum (Figs. 37 and 39) reveals a striking similarity in the shape and sequence of these organelles. In both cases they are (from left to right): contractile vacuole, longitudinal furrow, micronucleus and macronucleus. Two alternative explanations can be given to this phenomenon:

(1) As the longitudinal furrow of Diplodinium is situated on its right body-side, whereas in E. simulans (and in other species of Entodinium) it is situated on the left body-side, the furrow of Diplodinium is not homologous to the left lateral groove of Entodinium. The similarity in topographic interrelations of the nuclear apparatus,

longitudinal folds, and contractile vacuoles in these two genera is a mere coincidence and therefore of no significance.

(2) The similarity of topographic relationships of the nuclear apparatus, longitudinal fold and the contractile vacuoles in Entodinium of the caudatum-laterale group on the one hand, and in Diplodinium s. str. on the other is not accidental. The right lateral furrow of Diplodinium s. str. is homologous to the left lateral groove of Entodinium. The "right" body-side of Diplodinium is homologous to the left body-side of Entodinium.

The acceptance of the second thesis implies the following conception of the origin of the higher Ophryoscolecidae:

Primitive representatives of the genus Diplodinium s. str. originated from ancestors similar to existing species of Entodinium of the caudatum-laterale group in such a way that the contractile vacuole, the nuclear apparatus and the furrow-shaped left lateral groove were shifted ventrad across the left body-side. The oesophagus followed the macronucleus. The apex of the left lateral furrow moved ventrad, separated the ventral membranelle row ("dorsal" zone) from the oral apparatus and was transformed in the operculum. The ventral side of Entodinium became "dorsal" side of Diplodinium.

Phylogenetic phenomena, required by this conception, are based on evolutionary trends, observed in the "caudatum-laterale" group of Entodinium -- trends to the transformation of the left lateral groove into a narrow furrow and to the ventrad displacement of the contractile vacuole (see Part I of the present paper).

The following evolutionary steps can be traced from a study of existing species of the Ophryoscolecidae:

	Evolutionary Steps	Existing Species similar to Ancestral Forms
1.	Primitive species of *Entodinium* with elongate body without caudal spination and lateral groove.	*E. elongatum*, *E. nanellum* (Fig. 34) and others
2.	Origin of forms with caudal spination of the *E. caudatum* type possessing a wide and comparatively short left lateral groove.	*E. caudatum* (Fig. 35)
3.	Increase in length of the left lateral groove and ventrad shift of the contractile vacuole (cf. 7, p. 519).	*E. laterale*, *E. rectangulatum* (Fig. 36)
4.	Left lateral groove becomes transformed into a narrow furrow, which extends to the anterior margin of the outer adoral lip and separates the contractile vacuole from the nuclear apparatus.	*E. simulans* (Fig. 37)
5.	Further ventrad shift of the nuclear apparatus, left lateral furrow and contractile vacuole. The fold, produced by the anterior end of the left lateral furrow on the outer adoral lip, moving ventrad, separates the ventral membranelle row ("dorsal zone") from the adoral membranelle	

	zone and becomes the operculum. The oesophagus follows the macronucleus. Advent of second contractile vacuole.	Missing link (Fig. 38)
6.	Shifting further ventrad, the contractile vacuoles reach the ventral side of the body. As the angular velocity of rotation of the macronucleus is lower near the oral end, the macronucleus becomes flexed (boomerang-shaped). Left lateral furrow still persists.	*Diplodinium* (Fig. 39)
7.	Further ventrad shift of the nuclear apparatus. The "skeleton" appears on the track of the macronucleus.	*Eudiplodinium* (Fig. 40), *Eremoplastron*
8.	Disappearance of the left lateral furrow and pressing of the macronucleus between the contractile vacuoles. Further development of the skeleton.	*Metadinium* (Fig. 41) and other genera of higher Ophryoscolecidae.

The essential point of our conception of the origin of the higher Ophryoscolecidae is the transformation of the ventral side of *Entodinium* into the "dorsal" side of *Diplodinium* as a result of ventrad shift of the vacuoles, left lateral groove and of the nuclear apparatus. These phenomena can be described as torsional displacement of these structures across the left side of the body. This torsion occurred early in the evolution of Ophryoscolecidae and resulted in the advent of the higher genera of this family. The stages of this process are shown on Figures 34 to 41 in which, however, all drawings, with the exception of Figure 38, are camera lucida drawings of existing species of Ophryoscolecidae. Figure 38

Fig. 34 -- *Entodinium nanellum* Dogiel 1921 (x 800).

Fig. 35 -- *E. caudatum* Stein 1859 (x 630).

Fig. 36 -- *E. rectangulatum* Kofoid and MacLennan 1930 (x 630).

Fig. 37 -- *E. simulans* sp..n. (x 630).

Fig. 38 -- Hypothetical ancestor of the genus *Diplodinium* s. str.

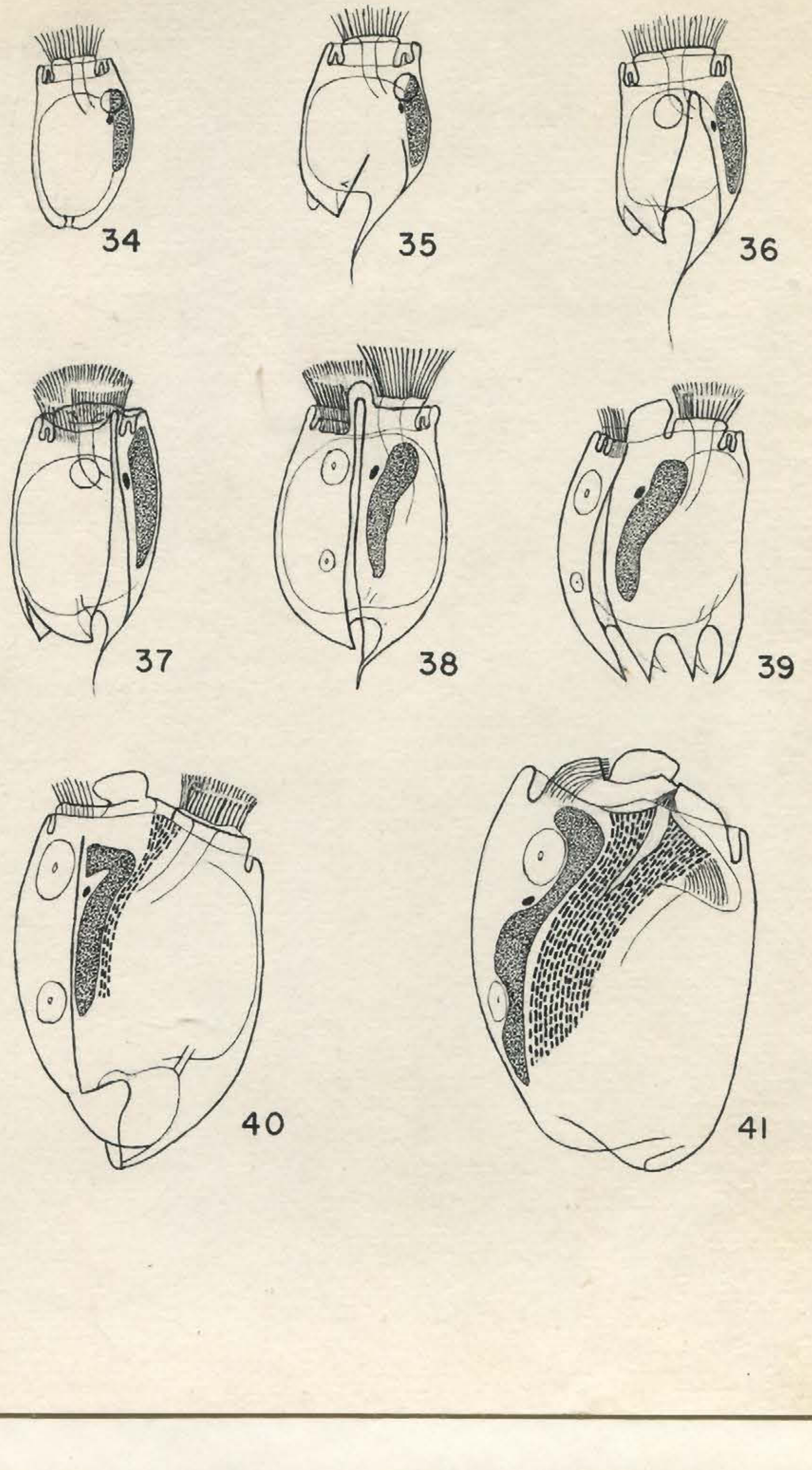
Fig. 39 -- *Diplodinium dentatum* (Stein 1859) Schuberg 1888 (x 450).

Fig. 40 -- *Eudiplodinium maggii* (Fiorentini 1889) (x 330).

Fig. 41 -- *Metadinium tauricum* (Dogiel et Fedorowa 1925) (x 275).

All figures, with the exception of Fig. 38, are slightly schematized camera lucida drawings of fixed and mounted specimens of Ophryoscolecidae from sheep and goats, from material collected by the author in Rawalpindi, W. Pakistan, in 1950-1954.

Drawings are made at different magnifications to reduce the progressive increase in size from Fig. 34 to Fig. 41.



Figs. 34-41.

represents a hypothetical ancestor of the higher Ophryoscolecidae. The comparison of the left side-view of E. simulans with the "right" side-view of Diplodinium dentatum (Figs. 37 and 39) makes the gap between the genera Entodinium and Diplodinium appear much smaller than it is usually believed to be. These phylogenetic phenomena can be compared to the processes of torsion (with subsequent detortion) frequently occurring in the life cycle of apostomatous ciliates. Indeed, the figures, representing the formation of the hypertomite in Phoretophrya nebaliae (Lwoff, 1950, p. 54) could serve as a good illustration of the origin of the genus Diplodinium.

In terms of the usual terminology the following table of homologies between Entodinium and Diplodinium can be compiled:

Entodinium	Diplodinium
Dorsal side	Ventral side
Left side	Right side
Ventral side	Dorsal side
Right side	Left side
Left lateral groove	Right cuticular furrow
Dorsal spine	Ventral spine

This last point seems to be of special interest for some aspects of the problem of morphological parallelisms in the family Ophryoscolecidae. Discussing this problem, Dogiel (1927, p. 280) states, that there is no parallelism in the structure of caudal spination in three-spined species of the genus Entodinium on the one hand and three-spined species of Diplodinium, Epidinium and Caloscolex on the other, because in *Entodinium* the longest spine is always the dorsal one, whereas in the above-mentioned genera of the higher Ophryoscolecidae the longest spine is the ventral. From our standpoint, however, the so-called ventral spine of the higher Ophryoscolecidae is a homologon of the dorsal spine of *Entodinium*. Therefore the facts, which, from Dogiel's standpoint, disprove the presence of parallelism between *Entodinium* and the higher Ophryoscolecidae, are from our standpoint a proof of the existence of such parallelism.

The new conception of the origin of the higher Ophryoscolecidae may provide a new approach to the evaluation of morphological parallelisms in this family and probably a new basis for the study of comparative morphology of this group. An attempt to reconstruct the phylogeny of the family Ophryoscolecidae on the basis of the new conception will be made in the third part of this paper.

PART III

PHYLOGENY OF THE OPHRYOSCOLECIDAE BASED ON THEIR COMPARATIVE MORPHOLOGY.

"Terms of art ... may seem to correct the wrong acceptance of words; yet all this is insufficient to prevent the seducing incantations of names in numerous respects, their doing violence to the understanding, and recoiling upon it, from whence they proceeded."

F. Bacon, Advancement of Learning, 1605.

1. Torsion as the Basic Phylogenetic Trend in the Family Ophryoscolecidae

In the second part of this paper we have discussed the interrelations between Entodinium of the caudatum-laterale group and Diplodinium s. str., and concluded, that the last genus originated from ancestors similar to Entodinium simulans as result of torsion, which displaced the nuclear apparatus, the left lateral groove, and the contractile vacuole of Entodinium from the dorsal side to the ventral, and that therefore the so-called "dorsal" side of the higher Ophryoscolecidae is homologous to the ventral side of Entodinium. In the present part an attempt is made to reconstruct the phylogeny of the Ophryoscolecidae on the basis of this conception.

The literature on the problems of the phylogeny of the Ophryoscolecidae is scant. Only two papers are concerned with it: a paper of Crawley, published in 1923, and that of Dogiel, published in 1946. Crawley's paper is at present to a considerable extent outdated. Many morphological features of the Ophryoscolecidae, on which his views were based, as e.g. the presence of a pit in the middle of the dorsal zone, and of a row of cilia, connecting the "dorsal" zone to the adoral, the production of cysts by these ciliates -- were shown to be non-existing. Crawley's conception of the evolution of this family has been summarized by him as follows:

> "Generic distinctions (in the Ophryoscolecidae, Aut.) are based on the form of the ciliary apparatus; specific -- on the size and the nature of the armature which is present on the posterior end of nearly all the species. These two sets of characters vary independently, thus bringing about the unusual phenomenon of a change of genus without any change of species. This is shown with almost the precision of a mathematical demonstration for Entodinium and Diplodinium, and would probably also be shown in the same way for Diplodinium and Metadinium were our knowledge of this last genus as extensive as that of the other two."

A detailed criticism of Crawley's paper seems to be now out of place. It may be stated, however, that he has confused parallel variable characters -- those of the caudal spination -- with specific characters and on this misinterpretation based his opinion on the "change of genus without any change of species". Dogiel's paper, published in Russian in 1946 and in English in 1947, is concerned with the "Phylogeny of Stomach-Infusorians of Ruminants in the Light of Paleontological and Parasitological Data". Analyzing the host-specificity of different genera and species of the Ophryoscolecidae, Dogiel came to the conclusion, that the genera Entodinium and Anoplodinium originated probably in Eocene, Epidinium and Eudiplodinium in Oligocene, Ostracodinium in Miocene, Caloscolex, Opisthotrichum, Ophryoscolex and Polyplastron in Pliocene. He states that "different genera of Ophryoscolecidae may be very easily arranged in a gradually ascending line of progressive evolution, illustrated by several systems of organelles. In this way the ciliary apparatus, originally consisting of a simple oral zone, becomes completed by another, dorsal zone; the number of contractile vacuoles gradually increases; skeletal plates, primarily wanting, later appear and increase in number and size; the posterior end of the body gradually develops a more and more complex array of caudal spines."

"On the first step of this evolutionary ladder has remained the genus Entodinium: a simple adoral zone of membranelles, one contractile vacuole, no skeletal plates, and weakly developed caudal spines are the characteristics of this genus."

"The second stage of the evolution is occupied by the genus Anoplodinium, possessing two ciliary zones, two vacuoles, but lacking the skeletal plates; the caudal spines are slightly more developed than in Entodinium."

"The third grade of morphological evolution is reached by the genus Eudiplodinium possessing two ciliary zones, two vacuoles, 1-2 narrow skeletal plates, and a scanty caudal armature."

"The fourth link of our morphological chain includes the genera Epidinium, Ostracodinium, and Opisthotrichum; they exhibit two ciliary zones, 2-4 vacuoles, 1-3 broad skeletal plates covering the best part of the right side of the body, and well developed caudal spines."

"The fifth and the last stage of evolution is represented by Polyplastron, Caloscolex, and especially by Ophryoscolex. These genera possess two ciliary zones, a large number of vacuoles (7-15) often arranged in 1 or 2 transverse rows, a highly developed skeleton consisting of 3-5 plates; the caudal spines reach in the genus <u>Ophryoscolex</u> their strongest development, forming from two to four concentric crowns." (See Dogiel 1947b, p. 337-338.)

Dogiel's description of the evolutionary steps in the phylogeny of the family Ophryoscolecidae is illustrated in the Russian version (1946) by a scheme, which is, however, absent in the English version (1947a). This scheme was reproduced by Dogiel in his textbook of general parasitology (1948, p. 83, Fig. 60) and later in his textbook of general protozoology published in 1951 (1951, p. 430, Fig. 257). This last scheme is reproduced in Fig. VI of the present paper. As evident from the above citation and from the scheme of evolutionary steps in the phylogeny of the Ophryoscolecidae, Dogiel was not concerned with the interrelations between the genera and has only sketched the general increase in complexity of these ciliates in the course of their evolution. His considerations about the time of origin of different genera of the Ophryoscolecidae are based exclusively on data concerning the evolution of their hosts. The aim of the present paper is to analyze the interrelations between the genera of the Ophryoscolecidae on the basis of morphological data. This, however, necessitates a revision of some basic concepts of their morphology.

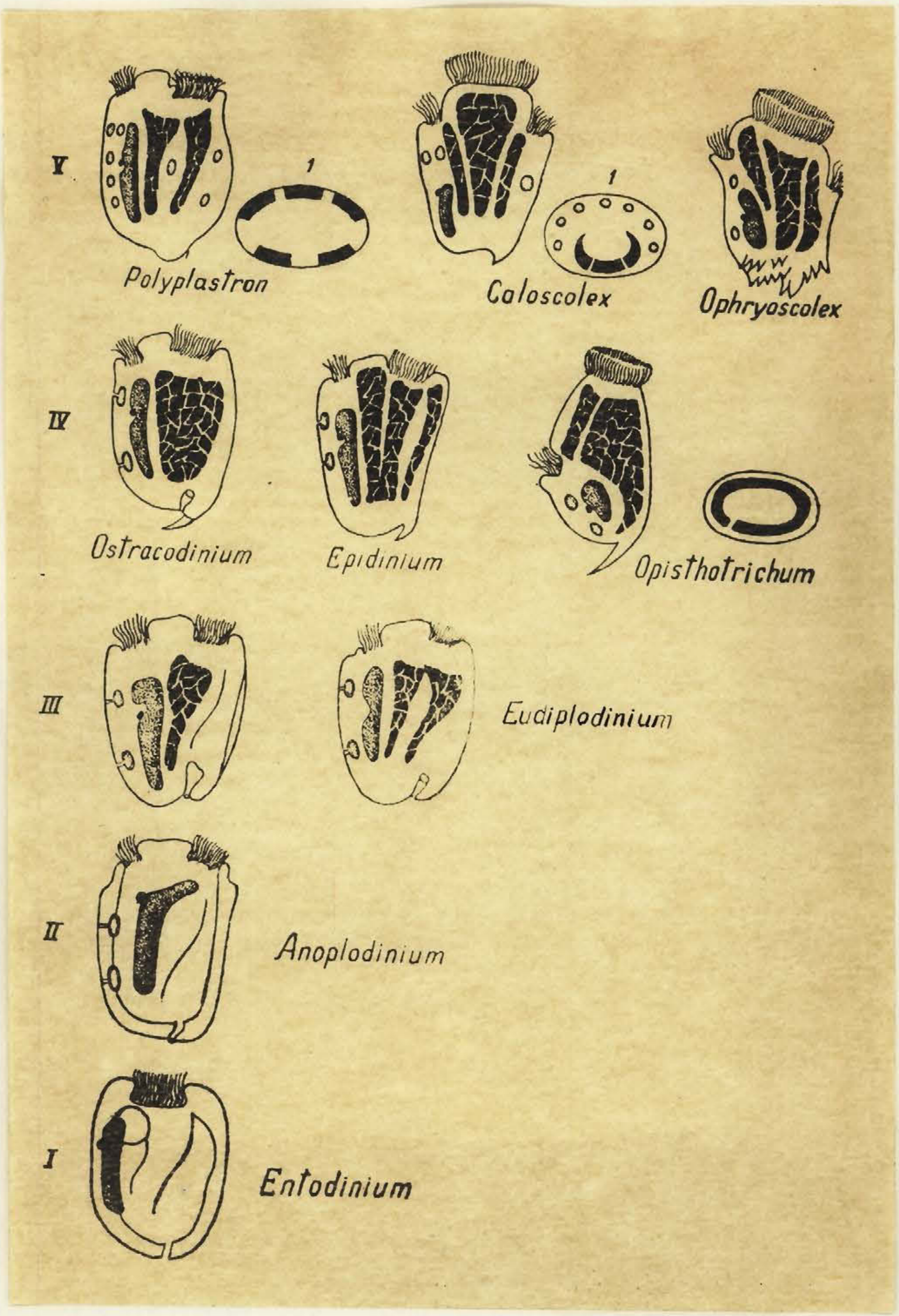


Fig. VI. Steps of progressive evolution in the family Ophryoscolecidae. (After Dogiel, 1951, Fig. 257)

2. Displacement of Structures and the Morphological Terminology

On comparing genera and species of the Ophryoscolecidae, we will have to use terms, designating their body-sides and body-surfaces. It is usual to designate as "dorsal side" the body-side marked by the macronucleus. In an early paper, published in 1925, Dogiel wrote: "Je rapporte le côté à macronucleus de l'*Entodinium* au côté macronucléaire des *Diplodinium* aplatis, c'est-à-dire au côté dorsal." Thus the dorsal side of *Entodinium* was defined as the side where the macronucleus is situated, and the identity of this side with the nuclear side of *Diplodinium* (sensu lato) was taken for granted. These views of Dogiel were shared by Kofoid and MacLennan who, five years later, wrote (1930, p. 475): "The side of the body (of *Entodinium*, Aut.), marked by the macronucleus, is considered the dorsal surface." In a subsequent paper on *Diplodinium* s. lato, published in 1932, these authors do not discuss the questions of promorphology of the higher Ophryoscolecidae, simply stating that "The morphology of the Ophryoscolecidae shows few basic differences from genus to genus" (l.c., p. 62). In his well-known monograph of the family Ophryoscolecidae published in 1927, Dogiel attempted to introduce another criterion for the recognition of the "dorsal" side -- the position of the contractile vacuole. These vacuoles are usually -- but not invariably -- situated near the macronucleus, and therefore the "dorsal" side so defined nearly always coincides with the "dorsal" side as defined by the position of the macronucleus. This criterion, however, is obviously not applicable to genera with numerous vacuoles arranged in transverse rows, as e.g. *Ophryoscolex*, *Caloscolex* and *Polyplastron* s. str.. Moreover, this criterion is confusing when strictly applied even within the limits of the genus *Entodinium*, because in *Entodinium* of the "*laterale*" group in the sense of Kofoid and MacLennan the vacuole is displaced ventrad and has shifted across the left body surface nearly 90° from the macronucleus. Dogiel's criterion of the "dorsal" side as the side where the vacuoles are situated, was probably intended to circumvent the difficulties arising in the identification of the dorsal side of *Diplodinium* s. str. (Dogiel's subgenus *Anoplodinium*) in which, as Kofoid and MacLennan put it (1930, p. 67), the macronucleus is located "near the middle of the right surface". Although the use of the position of the vacuoles as a criterion for the identification of the "dorsal" side of *Diplodinium* s. str. made its location in this particular genus unambiguous, it created serious difficulties in the identification of the dorsal side in the genera *Ophryoscolex* and *Caloscolex* (*vide supra*), and, moreover, tended to obscure the heuristic value of the unusual position of the macronucleus in *Diplodinium* s. str., this most primitive genus of the higher Ophryoscolecidae. However, the designation of the nuclear side of *Entodinium* as the "dorsal" side, generally accepted now, is of comparatively new origin. Stein (1859 a and b), and Schuberg (1888) designated as "dorsal" the body-side of Entodinium now called right side. It has to be remembered, that these early authors described as "ventral" side the side of Entodinium to which the mouth is slanted. And as it is slanted (in the terms of the present-day nomenclature) both ventrad and to the left, at least two body-sides of this ciliate can be with equal right termed "ventral". The Entodinium, as well as the vast majority of other ciliates, are asymmetrical organisms, swimming in spirals, the body rotating on its own axis and simultaneously revolving around the axis of progression. Trying to establish the body axes of this asymmetrical, spirally-moving organism, a protozoologist feels himself in the position of Alice before the mushroom trying to decide which side is which. It is clear, that the designation "dorsal side", when applied to Ophryoscolecidae, is only a convention. This term, transferred from the morphology of bilaterally-symmetrical organisms into the morphology of the Ophryoscolecidae nearly a century ago, has carried with it not only its direct meaning, but also a complex of associated ideas, which -- consciously or unconsciously -- were accepted by all subsequent students of these ciliates. The term "dorsal side" implied the notion of permanency of the side termed "dorsal". The homology of the "dorsal side" of Entodinium to the "dorsal" (nuclear) side of the higher Ophryoscolecidae was accepted by protozoologists as being self-evident, and was never questioned. In 1925 Dogiel has not questioned the homology of the dorsal (nuclear) side of *Entodinium* with that of *Diplodinium* (*vide supra*), nor has he questioned it in his text-book of general protozoology, written 26 years later (1951) in which, among other matters, he discusses the problems of evolution of the Ophryoscolecidae. For Kofoid and MacLennan (1932), the homology of the dorsal sides of *Entodinium* with that of the higher Ophryoscolecidae was also beyond doubts. It was, to use Bacon's expression, the "seducing incantation" of the words "dorsal side" which made protozoologists believe in the permanency and immutability of the side, so termed.

The irrational belief in the immutability of the position of the nuclear apparatus in the family Ophryoscolecidae has had also some practical consequences, which, in their turn, adversely influenced the development of the taxonomic studies of this family. The belief in the immutability of what was termed "dorsal" side of the Ophryoscolecidae resulted in the usage to depict representatives of this family always from the "same" side -- the right side of *Entodinium* and the so-called "right" side of the higher Ophryoscolecidae. In his monograph of the family Ophryoscolecidae Dogiel says (1927, p. 33): "Um den Vergleich der verschiedenen Formen zu erleichtern, haben wir alle Vertreter der Familie von einer und derselben, und nämlich von der rechten Seite abgebildet. Ich würde sämtlichen Ophryoscolecidenforschern raten, diesem

Beispiel zu folgen. An der rechten Körperseite sind die meisten Organellen der Ophryoscolecidae gelagert (wie der Kernapparat, Schlund, Afterröhre, Skelett), während die linke Körperhälfte hauptsächlich vom Entoplasmasack eingenommen ist." This is true in respect to the higher Ophryoscolecidae. However, the custom of depicting these ciliates from the "right" side resulted in comparing the right side of Entodinium with the "right" side of the higher Ophryoscolecidae, and lead therefore to lack of interest in such important structures of Entodinium as the left lateral groove and the position of the contractile vacuole. This is why the obvious similarity between the left lateral groove of Entodinium and the "right" dorsal furrow of Diplodinium s. str. has remained unnoticed, as was the close similarity of the sequence of organelles on the left body-side of Entodinium on the one hand, and on the "right" body-side of Diplodinium on the other, this sequence being in both cases from left to right: macronucleus, micronucleus, longitudinal furrow, contractile vacuole. The customary comparison of the right body-side of Entodinium with the "right side" of Diplodinium has necessarily lead to the conclusion that this last genus originated from Entodinium as result of the following changes:

1. The micronucleus was displaced "dorsally" to the macronucleus.
2. The contractile vacuole was displaced "dorsally" to the nuclear apparatus.

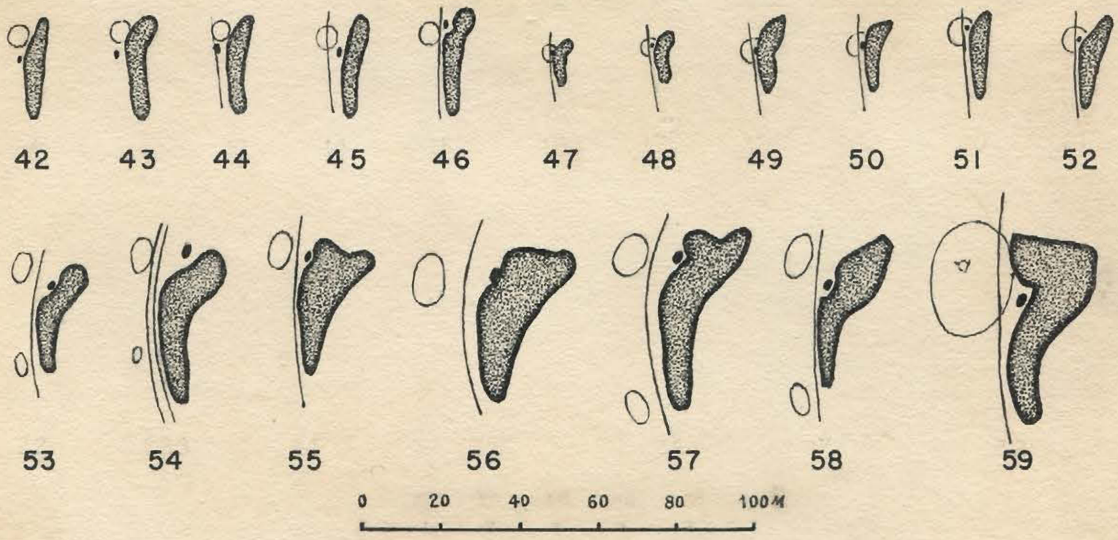
3. The operculum was formed, which
4. Separated the adoral membranelle zone into the adoral and "dorsal" zones.

The interdependence of these processes is not explained by the usual theory of the origin of the higher Ophryoscolecidae nor does this theory explain the peculiar position of the nuclear apparatus in Diplodinium s. str., in which this apparatus is situated in the middle of the "right" side of the body. This theory also does not explain the presence of a longitudinal cuticular fold between the nuclear apparatus and the contractile vacuoles in Diplodinium s. str. and in other primitive genera of the higher Ophryoscolecidae. This fold, so peculiar for these genera, being irrelevant from the standpoint of the usual theory of the origin of the higher Ophryoscolecidae, is not represented on Dogiel's scheme of the steps of progressive evolution of this family (see Fig. VI, p. 77 of the present paper). Although the longitudinal fold (furrow) is represented on Kofoid and MacLennan's drawing of D. dentatum (1932, p. 64, Fig. A), it is not named in the legend, and not mentioned in the description of morphology of this species -- probably because of its irrelevancy.

3. Displacement of Structures and the Phylogenetic Interrelations of Genera

In the second part of this paper we have shown, that *Diplodinium* s. str. originated from ancestors similar to *E. simulans* as the result of torsion, which displaced the contractile vacuole, the left lateral groove, and the nuclear apparatus from the nuclear side of *Entodinium* to the opposite body-side. The displaced structures have undergone a rotation of about 90-100° around the longitudinal body axis; as a result of this torsion the contractile vacuole, situated in *Entodinium* of the "*laterale*" group on the level of the oesophagus was shifted to the "ventral" side of the body (*vide supra*, p. 69, Figs. 37-39). The nuclear apparatus was displaced from its original position to the middle of the left body-side. The slit-shaped left lateral groove shifted with these organelles, preserving its position between the nuclear apparatus and the contractile vacuole. The anterior end of this groove, which already in *E. simulans* extends to the anterior margin of the outer adoral lip, has, in the course of its ventrad shift, produced the operculum as an excrescence of the distorted adoral lip. The posterior end of the ciliate, has, however, not participated in the rotation. If this conception is correct, one may expect that the configuration of organelles (nuclear apparatus and contractile vacuoles) on the dorsal side of *Entodinium* of the "*laterale*-

caudatum" group should be similar to the configuration of these organelles on the "right" side of Diplodinium s. str. (which from our standpoint, is homologous to the left body-side of Entodinium). Figures 42 to 52 represent "dorsal" views of the nuclear apparatus, contractile vacuoles, and of the dorsal edge of the left lateral groove of several species of Entodinium. The lower row (Figs. 53-59) represents the nuclear apparatus and the contractile vacuoles of five species of Diplodinium and of one species of Eudiplodinium, viewed from the "right" side. The similarity in the relative position of the represented organelles and in the shape of the macronucleus is obvious. It becomes still more marked in cases when drawings are made from young specimens of Diplodinium and Eudiplodinium which possess only one contractile vacuole (Figs. 55, 56 and 59). The similarity between the relative position of the edge of the left lateral groove in Entodinium and the "right dorsal" furrow in Diplodinium is obvious. The resemblance of the dorsal aspect of Entodinium to the "right" lateral aspect of Diplodinium becomes still more obvious if we compare outlines of whole animals. Figures 60 to 62 represent dorsal aspects of three species of Entodinium (E. longinucleatum, E. rectangulatum, and E. caudatum), Figures 63 and 64 -- "right" lateral aspects of Diplodinium crista-galli and D. laeve. (It is remarkable that the presence of the "right" lateral furrow in

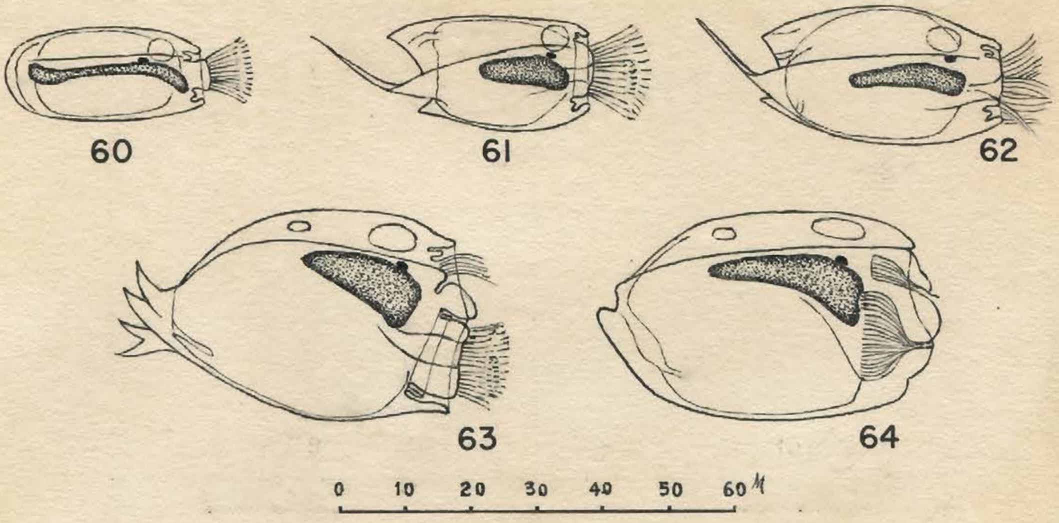


Figs. 42-52 -- "Dorsal" view of the nuclear apparatus, left lateral groove, and contractile vacuole of *Entodinium*.

Figs. 53-59 -- "Right" lateral view of the nuclear apparatus, "right" dorsal furrow and contractile vacuoles of *Diplodinium* and *Eudiplodinium*.

Figs. 42-46 -- *E. caudatum*; Figs. 47 and 48 -- *E.* cf. *loboso-spinosum*; Figs. 49 and 50 -- *E. rectangulatum*; Figs. 51 and 52 -- *E. simulans* f. *caudatum*; Fig. 53 -- *Diplodinium dentatum*; Fig. 54 -- *D. anacanthum*; Fig. 55 -- *D. minor*; Figs. 56 and 57 -- *D. crista-galli*; Fig. 58 -- *D. penthacanthum*; Fig. 59 -- *Eudiplodinium maggii*.

All drawings were made with the aid of the camera lucida from stained and mounted material from sheep and Jamnapari goats, collected in Rawalpindi, W. Pakistan, in 1950-1954.



Figs. 60-62 -- Dorsal aspects of Entodinium.

Figs. 63 and 64 -- "Right" lateral aspects of Diplodinium.

Fig. 60 -- E. longinucleatum; Fig. 61 -- E. rectangulatum;
Fig. 62 -- E. caudatum; Fig. 63 -- D. crista-galli;
Fig. 64 -- D. laeve.

the last two species is not mentioned in their description in Dogiel's monograph of the Ophryoscolecidae.)

From our standpoint *Diplodinium* is a contorted *Entodinium*, in which the organelles, situated near the "dorsal" side of *Entodinium*, are displaced to the left body-side. This explains the similarity between the left (usually called "right") side of *Diplodinium* s. str. and the dorsal (nuclear) side of *Entodinium*. This torsional displacement of structures is the cause of the similarity in the relative position of organelles on the ventral ("dorsal") side of *Diplodinium* and the left body-side of *Entodinium*. The resemblance, e.g. of the "dorsal" view of *D. dentatum*, represented by Kofoid and MacLennan (1930, p. 70, Fig. B6) with the left lateral view of *E. simulans* (see Figs. 65-67 of the present paper) is striking. The similarity between the "dorsal" aspect of *Diplodinium* s. str. and the left lateral aspect of *Entodinium* may possibly be the cause of the persistence in the protozoological literature of a non-existing species of *Entodinium* -- the *E. dentatum* Stein 1859. This species was depicted by Eberlein (1895)(his drawing is reproduced by Crawley, 1923, plate 28, Fig. A2 and by Dogiel, 1927, p. 66, Fig. 33; see Fig. VII of the present paper). It was not seen since 1895. Dogiel (1927), discussing the morphology of *E. dentatum*, states that its micronucleus "nach Eberlein liegt dorsal vom vorderen Drittel des Macronucleus, was für uns ganz unglaublich erscheint". Another peculiarity of

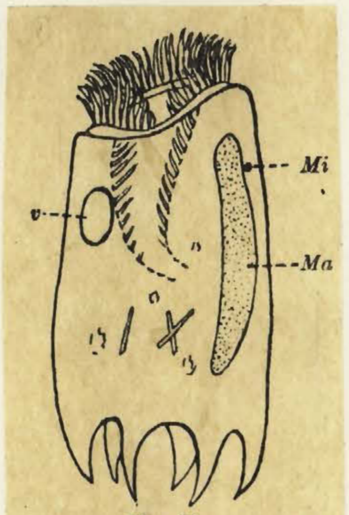


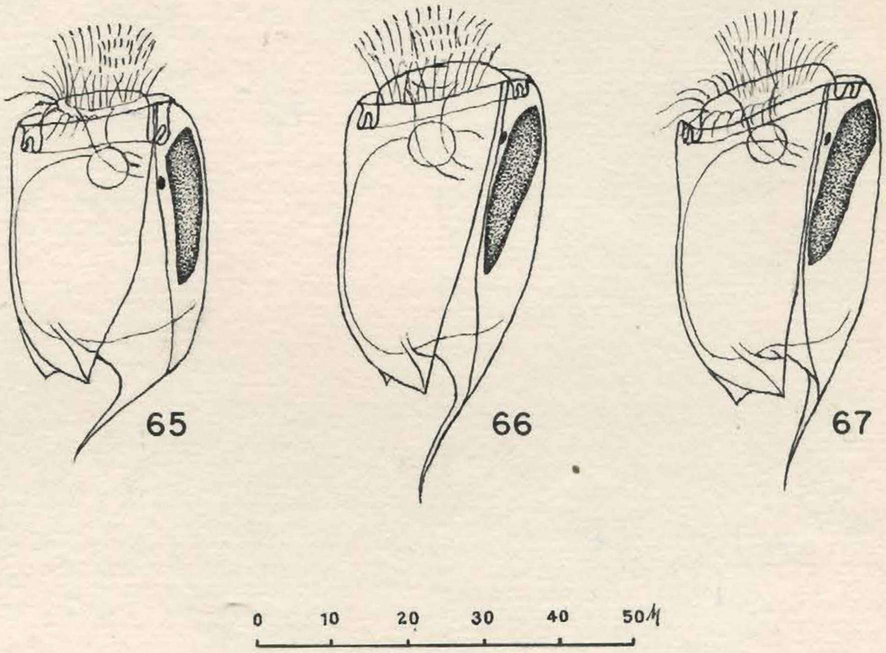
Fig. 33.
Ent. dentatum nach EBERLEIN.
Vergrößerung 750×.

Fig. VII

E. dentatum is its large size. According to Eberlein (1895) its length is 60-90µ, its width -- 30-50µ. The measurement of Eberlein's Figure 21 (of his plate 19, see Fig. VII of the present paper) gives the body length as 80µ, that of the caudal spination as 20µ. The length of Diplodinium dentatum is, according to Dogiel, 55-70µ, not including the length of the caudal spination. Thus, contrary to what can be expected, E. dentatum is slightly larger than Diplodinium dentatum. All these peculiarities of E. dentatum can be explained if we assume that Eberlein's figure of this species is nothing else but a drawing of the ventral ("dorsal") aspect of Diplodinium dentatum, and that E. dentatum does not exist.

On studying the morphology of *E. rectangulatum* and *E. simulans* we have seen, that in these species the contractile vacuole is displaced ventrad to the level of the oesophagus and separated from the nuclear apparatus by the anterior portion of the left lateral groove. The examination of numerous specimens of *E. simulans* from the faunule of the sheep 54 as well as from other faunules has shown, that the position of the nuclear apparatus in this species is slightly variable and that in some specimens the posterior end of the macronucleus is shifted ventrad (see Figs. 66 and 67). This ventrad displacement of the macronucleus is accompanied by a narrowing of the caudal end of the left lateral groove (compare Figs. 65, 66 and 67). The similarity between the left body-side of such specimens of *E. simulans* and the "right" body-side of *Diplodinium* s. str. is striking.

Comparing the structure of *E. simulans* and of other related species of this genus not only with that of *Diplodinium* s. str., but also with the structure of other genera of the higher Ophryoscolecidae, we notice that the ventrad shift, which has displaced the nuclear apparatus to the middle of the left body-side in *Diplodinium* s. str. is proceeding further in other genera of this family, shifting the nuclear apparatus to the "ventral" side of these ciliates. This ventrad shift is accompanied by progressive development of the skeleton and, to a certain degree, by progressive increase in body-size.



Figs. 65-67 -- *E. simulans* sp. n. Variations in the position of the nuclear apparatus and the shape of the left lateral groove.

Torsion of the body in some genera of the Ophryoscolecidae was known a long time ago. Dogiel in his monograph of the family Ophryoscolecidae (1927) describes the torsion of the anterior part of the body of *Opisthotrichum* (l.c., p. 221), and the rotation of the skeleton of *Caloscolex* (l.c., p. 212). Kofoid and MacLennan (1933, p. 2), describing the morphology of *Epidinium*, state that "the main longitudinal axis is twisted, the anterior end of the body being bent ventrally and twisted to the right about the main axis. This twisting is particularly clearly shown in a dorsal view and involves the position of the skeletal plates, nuclei, contractile vacuoles, and spines as well as the general contours of the body. In other genera, such as *Diplodinium*, *Eudiplodinium*, and *Ostracodinium*, the body shows very little, if any, twisting around the main axis."

However, the torsion is not an accidental morphological trait of a few genera of the Ophryoscolecidae, but the basic evolutionary process in the phylogeny of this family. Higher Ophryoscolecidae originated from ancestors similar to existing species of the "*laterale*" group of *Entodinium* as a result of torsional displacement of structures, which produced a new type of organization endowed with high potential for further evolution. This major event in the phylogeny of the Ophryoscolecidae has to be regarded as an aromorphosis, breaking way for further progressive development of this group. Although Dogiel was not aware of the rôle of torsion in the evolution of the Ophryoscolecidae, he wrote: "Examining the picture of these complications (in the evolution of this family) we notice that they comprise such a diversity of characters, and are accompanied by such an intensification of functions, that the whole ladder of the progressive changes in the course of evolution of the family in some way does not fit in the frame of idioadaptation" (1951, p. 429).

The development of the skeleton and of the caudal spination is closely connected with the grade and character of torsion, as well as the shape and size of the body. The relations between different genera of the Ophryoscolecidae and the position of these genera in the dendrogramme of the family, can be determined on the basis of the following characters:

1. The degree of torsion, i.e. the degree of the ventrad shift of the nuclear apparatus.
2. The distance between the oral and the ventral ("dorsal") zone of membranelles.
3. The development of the skeleton.
4. The grade of polymerisation of organelles.
5. The size of the body.

A dendrogramme of the family Ophryoscolecidae, based on these criteria, is represented on Plate 1. The most primitive genus of this family is beyond any doubt the genus Entodinium (Dogiel 1923, 1927; Crawley 1927). This genus has only one zone of membranelles -- the adoral -- and one contractile vacuole. It contains over 80 species, some of which, however, may prove to be forms produced by intraspecific variability of some plastic species. Although the family Ophryoscolecidae (with the exception of Polydiniinae) is confined to ruminants -- Pecora and Tylopoda -- the genus Entodinium contains one species parasitizing rodents -- E. lemmi Kopperi 1935 and one species inhabiting the colon of the Indian rhinoceros -- E. insolitum Watson 1945. All other species parasitize ruminants, and, with the exception of one species found in camels (E. ovum-rajae Dogiel, 1926), are confined to hosts of the suborder Pecora. All species of this genus are asymmetrical, the asymmetry being an ancestral character of this genus. Bilateral symmetry -- at least in the outer shape of animals -- is imposed on them by the requirements of locomotion in straight lines, and was probably never proper to the ancestors of the Ophryoscolecidae. Many species of Entodinium obviously possess an asymmetrical body-shape adapted for spiraling, their spines, flanges and grooves being spirally contorted. Such adaptations are very prominent in Entodinium of the "biconcavum" group, and specially in E. tricostatum, but are more or less expressed in all species of this genus. Effective spiraling may facilitate penetration of Entodinium into lumps of food swallowed by the host and thus be of survival value for these ciliates. Although spiral structure is more or less marked in all species of Entodinium, the ventrad displacement of the contractile vacuoles is present only in four species of this genus: E. rectangulatum, E. laterale, E. simulans and probably in E. ovale, described by Jameson (1925). In a small percentage of specimens of E. simulans the nuclear apparatus also becomes slightly displaced ventrad (vide supra, Figs. 66 and 67). Diplodinium, according to our conception, originated from ancestral forms similar to E. simulans as the result of further ventrad shift of the contractile vacuole, the left lateral groove, and of the nuclear apparatus. A hypothetic ancestral form of Diplodinium is represented in Plate I, Figure 7. This form was discussed in more detail in the second part of the present paper. The anterior end of the left lateral groove, distorting the outer adoral lip, has formed the operculum, and has pushed ventrad the outer row of membranelles of the adoral zone. This row in the hypothetical ancestor is still continuous with the adoral zone. Further torsion resulted in the severance of the displaced row of membranelles from the adoral zone and in further ventrad shift of the nuclear apparatus. Thus the genus Diplodinium originated -- a genus differing from Entodinium not only in its structure, but also in its size and its food habits. Most species of Diplodinium are larger than an average Entodinium, and ingest plant fibres which they digest with the aid of cellulolytic ferments (although it is not clear whether these ferments are produced by the ciliates themselves or by associated bacteria). The increase in body-size, permitting to engulf and digest larger particles of cellulose, may be of survival value for larger individuals, and therefore provide a base for the progressive increase in body-size in the evolution of cellulose-ingesting genera of the Ophryoscolecidae, genera differing from the primitive genus Entodinium both morphologically and physiologically. The most important peculiarity of the higher Ophryoscolecidae, from the morphological point of view, is the position of the nuclear apparatus, which, in terms of the usual terminology, marks the position of the "dorsal side". The use of this terminology in discussing the comparative morphology of Entodinium on the one hand, and of the higher genera of the family on the other, shall inevitably result in confusion of the nuclear ("dorsal") side of Entodinium with the nuclear ("dorsal") side of the higher Ophryoscolecidae, which are not homologous. Therefore in the subsequent discussion of the comparative morphology of this family, we shall use the term "primary nuclear side" or "dorsal side" to designate the nuclear ("dorsal") side of Entodinium. It has to be remembered that the antinuclear side of the higher genera is homologous to the nuclear side of Entodinium. The row of membranelles, severed from the adoral zone and shifted away from the mouth -- row, usually termed "dorsal zone" -- will be designated as "metoral zone" -- a neutral term not connected with necessarily conventional designations of the body-sides. To facilitate the comparison of our descriptions with those of previous authors, we shall quote in brackets the corresponding terms of the usual terminology.

In the genus *Diplodinium* s. str. (*Diplodinium* Schuberg emend. Kofoid and MacLennan) the nuclear apparatus is situated half-way between the primary and the secondary nuclear side near the middle of the left ("right") body-surface (see plate 1, Fig. 8). As the grade of torsion decreases from the equator towards the poles of the body, the macronucleus becomes flexed and assumes the shape of a boomerang. The left lateral groove persists as a narrow furrow situated between the contractile vacuoles and the nuclear apparatus. Due to the torsion of the endoplasmic sac the anus opens into the posterior portion of the left lateral groove. The ventrad shift of the dorsal fold of this groove transforms its posterior portion into a wide funnel, into which the anus opens. The anus of *Diplodinium* s. str. and of other genera of the higher Ophryoscolecidae is therefore homologous to the anus of *Entodinium* plus the caudal part of the left lateral groove. *Diplodinium* s. str. lacks a skeleton -- a feature which it shares with only one genus of the higher Ophryoscolecidae -- *Eodinium* Kofoid and MacLennan 1932.

This last genus (plate 1, Fig. 11) comprizes a few small species, in which the nuclear apparatus is shifted much farther ventrad ("dorsad") as in *Diplodinium* s. str., and touches the ventral ("dorsal") body-wall. This genus is therefore more advanced than *Diplodinium* s. str. and may have originated from this last as a result of further ventrad shift of the nuclear apparatus without the formation of a skeleton. However, it is possible also to regard this genus as being derived from a higher genus, e.g. *Metadinium*, as a result of a secondary loss of the skeleton and decrease in body-size. In any case *Eodinium* is not the most primitive genus of the higher Ophryoscolecidae, as its name may suggest.

The genus *Eremoplastron* Kofoid and MacLennan 1932 (see plate 1, Fig. 10) is the most primitive of all genera of the family, possessing a skeleton. This skeleton is represented by only one narrow plate -- the primitiva. In all other respects it closely resembles *Diplodinium* s. str.: the nuclear apparatus has not reached the ventral side of the body, and the left lateral groove still persists as a narrow furrow situated between the nuclear apparatus and the contractile vacuoles, although this furrow is usually (but not always) shallower than in *Diplodinium* s. str. The macronucleus is more or less straight but slanted in respect to the main body-axis, the posterior end of the macronucleus being much closer to the secondary nuclear side (the "dorsal" side), than the anterior. The trend to the production of caudal armature is far less expressed in *Eremoplastron* than in *Diplodinium* s. str.

The genus *Eudiplodinium* (plate 1, Fig. 9) is closely related to *Eremoplastron*, differing from it only in the shape of the macronucleus -- which can hardly be regarded as a good generic character. In this respect one may agree with Wertheim (1935) who proposed to fuse the genera *Eremoplastron*

Kofoid and MacLennan 1932 with Eudiplodinium s. str. into one genus, which, according to the priority law, has to bear the name Eudiplodinium Dogiel emend. Kofoid and MacLennan emend. Wertheim.

The genus Diploplastron Kofoid and MacLennan 1932 possesses two skeletal plates -- the primitiva and carina; however, his macronucleus is still at a considerable distance from the ventral body-side and not in contact with the vacuoles. The left lateral furrow is smoothened and nearly absent (see plate 1, Fig. 12).

In the genus Metadinium Awerinzew and Mutafowa 1914 emend. Kofoid and MacLennan 1932 (plate 1, Fig. 13) the skeleton is represented either by one wide plate split into two in its anterior part or by two comparatively wide plates. The macronucleus is shifted ventrad farther than in Eremoplastron and is partially pressed-in between the vacuoles. The left lateral furrow is completely absent. The average size of the species of Metadinium is much larger than that of Diplodinium and Eremoplastron.

A further stage of the ventrad shift of the nuclear apparatus is observed in Ostracodinium Dogiel 1927 emend. Kofoid and MacLennan 1932, in which the nuclear apparatus is closely pressed against the ventral body-side ("dorsal side") and has displaced the contractile vacuoles to the right ventral ("left dorsal") part of the body. Only in O. gracile (plate 1, Fig. 14), which probably is one of the primitive species of this genus, are the shape of the macronucleus and the position of the contractile vacuoles in the depressions of the nucleus reminiscent of conditions typical for the genus Metadinium. The skeleton is represented by one very long and wide skeletal plate extending under the entire left ("right") body-surface and transgressing to the dorsal ("ventral") side. Species with three skeletal plates, differing from all other species of this genus also in some other respects, have been separated by Kofoid and MacLennan (1932) into the genus Enoploplastron (plate 1, Fig. 17).

In the genus Polyplastron Dogiel 1927 emend. Kofoid and MacLennan 1932 the nuclear apparatus is still situated at some distance from the ventral ("dorsal") side of the body (plate 1, Fig. 15). This genus possesses a complex skeleton, consisting of five plates -- two comparatively wide plates on the left ("right") side of the body and three narrow inconspicuous plates on the right ("left") side. The contractile vacuoles are numerous and situated not only near the nuclear apparatus, but also on the left ("right") side of the body. The high degree of complexity is achieved in this genus not by further torsion, but by polymerization of the organelles -- skeletal plates and contractile vacuoles. The same applies to the closely related genus Elythroplastron Kofoid and MacLennan 1932 (plate 1, Fig. 16) which possesses only three contractile vacuoles situated near the macronucleus and three skeletal plates -- two on the left ("right") side of the body, and one at the right ("left") side of it.

All the above mentioned genera of the higher Ophryoscolecidae possess several common characters: their adoral and metoral ("dorsal") zones of membranelles are situated approximately at the same level; the multitude of their shapes depends mainly on the degree of torsion of their body and on the polymerization of organelles. In another group of the higher Ophryoscolecidae to these factors is added the elongation of the anterior part of the body between the oral and the metoral ("dorsal") membranelle zones.

One of the primitive genera of this second group of Ophryoscolecidae is Epidinium Crawley 1923 (see plate 1, Fig. 18). In this genus the anterior part of the body -- the "prezonal part" as Dogiel calls it -- has grown, the body has become elongated and the operculum stretched and smoothened. As a result of this growth the metoral ("dorsal") zone of membranelles is situated about one-fourth of the body-length behind the oral zone. Epidinium has a highly-developed skeleton consisting of three skeletal plates. This skeleton closely resembles that of Enoploplastron Kofoid and MacLennan 1932 (plate 1, Fig. 17). This last genus, consisting of only two species, has a skeleton composed of three plates, which in E. confluens (Dogiel 1925) are fused together. Its metoral membranelle zone ("dorsal zone") is situated behind the adoral zone and the operculum flattened and elongated. It is probable that this genus is related to the ancestors of Epidinium. The description of a new form of Enoploplastron, provided with a long caudal spine, similar to that of *Epidinium* -- *Enoploplastron triloricatum* f. *dissimilis* (Moriggi 1950)--supports this conception. However, the exact position of this genus within the family Ophryoscolecidae is not clear.

Other genera of this group -- *Ophryoscolex* Stein 1859, *Epiplastron* Kofoid and MacLennan 1933, *Opisthotrichum* Buisson 1923 and *Caloscolex* Dogiel 1926 -- probably originated from ancestors similar to *Epidinium*. The present writer has had no opportunity to examine representatives of the three last genera. The figures of *Opisthotrichum*, *Epiplastron* and *Caloscolex* (plate 1, Figs. 19, 20 and 22) are taken from Dogiel's monograph (1927), and brought to the scale of other figures of Plate 1.

Epiplastron (plate 1, Fig. 20), according to Kofoid and MacLennan (1933, p. 18), "appears to be an offshoot from *Epidinium* along the line of increase in the number of main skeletal plates from three to five and an increase in size of the whole skeletal complex".

Opisthotrichum Buisson 1923 (plate 1, Fig. 19) has probably originated from *Epidinium*-like ancestors as a result of caudad displacement of the short metoral ("dorsal") zone, which has pushed caudad the nuclear apparatus and the contractile vacuoles. The skeleton is represented by one very wide twisted skeletal plate.

One of the most highly organized genera of the Ophryoscolecidae is the type-genus of the family -- Ophryoscolex Stein 1859 (plate 1, Fig. 21). It has probably originated from Epidinium in the way of further development of the anterior body-part, resulting in the shift of the metoral zone ("dorsal zone") closer to the equator, in the lengthening of this zone, in the increase in the number of contractile vacuoles, and in further development of the caudal spination, which in this genus reaches the highest grade of complexity.

Caloscolex Dogiel 1926 (plate 1, Fig. 22) differs from Ophryoscolex in possessing a higher degree of torsion of the skeleton (Dogiel, 1927, p. 212), a longer metoral ("dorsal") membranelle zone, and in a lesser degree of development of the caudal spination. This genus has only one transverse row of contractile vacuoles, differing in this respect from Ophryoscolex, which has two rows of vacuoles.

Discussing the comparative morphology of the Ophryoscolecidae, we came to the conclusion, that in the course of the evolution of this family the nuclear apparatus and the contractile vacuole have shifted from the primary nuclear side (the dorsal side of Entodinium) to the secondary nuclear side (the "dorsal" side of the higher Ophryoscolecidae), a shift ranging from 100° to 180° on the circumference of the body. This conclusion was reached on the basis of comparison of numerous species of the Ophryoscolecidae ranging from the most primitive to the most complex forms. Discussing the basic morphological traits of different genera of this family, we have had to refer to the primary and secondary nuclear sides, these notions being based on the comparative study of numerous species. But for the purposes of identification of species in the course of every-day work, in which comparative material is often absent, we have to use some criteria permitting us to identify the position of the primary nuclear side in each individual ciliate, without resorting to comparative methods. Such means is provided by the constancy of the relative position of the micro- and macronucleus in the Ophryoscolecidae. In all genera of this family, whether primitive or advanced, the micronucleus is situated ventrally to the macronucleus, the term "ventral side" being a designation of the anti-nuclear side of the body of Entodinium and of the secondary nuclear side of the higher Ophryoscolecidae, these sides being homologous. A line, drawn from the centre of the micronucleus through the axis of the macronucleus and normal to that axis, will show the direction of the primary nuclear side. This applies, however, only to genera in which the torsion does not exceed 180°, but is not applicable to the subfamily Polydiniinae Kofoid 1935, possessing a much higher degree of torsion.

4. Grouping of Genera within the Family Ophryoscolecidae

The genera, briefly discussed above, despite their high diversity, are included in one family -- the Ophryoscolecidae -- and not grouped into subfamilies, although they obviously constitute several natural groups. Within the Ophryoscolecidae Kofoid has established one subfamily -- the Polydiniinae -- to include two genera of peculiar ciliates from an Indian elephant -- Polydinium and Elephantophilus Kofoid 1935. The remaining genera of the family were never subdivided into or united in a subfamily, although Bhatia in his book on Ciliophora of British India (1936, p. 275) states, that the subfamily Ophryoscolecinae was established by Kofoid in 1935, and characterizes this subfamily as follows:

"Subfamily Ophryoscolecinae Kofoid 1935. Ophryoscolecidae with an adoral membranelle zone and with or without a dorsal zone. One to five skeletal plates present. Contractile vacuoles usually one to twelve in number, located on the dorsal side adjacent to the macronucleus."

This characteristic of the subfamily Ophryoscolecinae obviously excludes from it all genera without skeleton, i.e. Entodinium, Diplodinium s. str. and Eodinium. On the other hand the statement, that the contractile vacuoles are located on the dorsal side adjacent to the macronucleus, would exclude from this subfamily the genera Ophryoscolex, *Caloscolex* and *Polyplastron*. A comparison of this characteristic of the subfamily Ophryoscolecinae, ascribed by Bhatia to Kofoid, with the text of Kofoid's paper of 1935 shows, that Kofoid has merely discussed in it the morphological characters of the *family* Ophryoscolecidae. "The Ophryoscolecidae", says Kofoid in this paper (1935, p. 502), "form a compact but structurally diversified assemblage characterized by an adoral membranelle zone, a heavy peripheral pellicle, permanently located excretory vacuoles, and a system of from *one to five vacuolated "skeletal" plates* arranged peripherally to the pharynx and projecting posteriorly along the side of the macronucleus. These plates are characteristic of all but a few of the most primitive genera of this family. A few of the higher genera, such as *Epidinium*, *Diplodinium* and *Ophryoscolex*, of the Ophryoscolecidae, add to the adoral zone of membranelles a second, always dorsal, membranelle zone, having no relationship to the feeding function, but accessory to the locomotor function." And further: "The excretory *vacuoles, from one to twelve in number, are located in the dorsal side adjacent to the macronucleus*, except in those cases where the vacuoles are numerous, in which instances they have a wider distribution." It is obvious, that Bhatia has compiled the diagnosis of the *subfamily* Ophryoscolecinae, the establishment of which he ascribes to Kofoid, from sentences, taken from Kofoid's description -- not diagnosis -- of the *family* Ophryoscolecidae.

Thus Kofoid can not be regarded as author of the diagnosis of the subfamily Ophryoscolecinae. Nor can Bhatia be considered as the author of this diagnosis, because he has obviously compounded it from Kofoid's sentences, taken from his discussion of morphological traits of the family Ophryoscolecidae. Besides that, Bhatia has badly distorted Kofoid's discussion by omitting several important points concerned with genera devoid of skeleton and with the position of the contractile vacuoles in some higher genera of the family. The whole incident with the diagnosis of the subfamily Ophryoscolecinae can therefore be simply dismissed as a vexatious misunderstanding.

All genera of the Ophryoscolecidae, discussed in the present paper, with the exception of the Polydiniinae, can be grouped into three following subfamilies:

1. Subfamily Entodiniinae, subf. nova.

One membranelle zone, one contractile vacuole. In side-view the macronucleus between the micronucleus and the nearest body-outline. Skeleton absent.

Type genus: Entodinium Stein 1859.

2. Subfamily Diplodiniinae subf. nova.

Two membranelle zones situated approximately in one transverse plane. Two or more contractile vacuoles. In side-view the micronucleus situated between the macronucleus and the nearest body-outline. Skeleton absent or present. Body more or less flattened.

Type genus: Diplodinium Schuberg 1888 emend. Kofoid and MacLennan 1932.

Other genera:

- Eodinium Kofoid and MacLennan 1932
- Eremoplastron Kofoid and MacLennan 1932
- Eudiplodinium Dogiel 1927 emend. Kofoid and MacLennan 1932
- Diploplastron Kofoid and MacLennan 1932
- Metadinium Awerinzew and Mutafowa 1914 emend. Kofoid and MacLennan 1932
- Polyplastron Dogiel 1927 emend. Kofoid and MacLennan 1932.
- Elytroplastron Kofoid and MacLennan 1932
- Ostracodinium Dogiel 1927 emend. Kofoid and MacLennan 1932
- Enoploplastron Kofoid and MacLennan 1932

3. Subfamily Ophryoscolecinae subf. nova.

Two membranelle zones situated in different transverse planes. Two or more contractile vacuoles. In side-view the micronucleus situated between the macronucleus and the nearest body-outline. Skeleton present. Body more or less cylindrical.

Type genus: Ophryoscolex Stein 1859.

Other genera:

- Epidinium Crawley 1923
- Opisthotrichum Buisson 1923
- Caloscolex Dogiel 1926
- Epiplastron Kofoid and MacLennan 1933

These three new subfamilies differ considerably in the grade and the character of torsion, as well as in some other respects. In the Entodiniinae -- the most primitive subfamily -- the torsion is absent or only slight marked (in the "caudatum-laterale" group of Entodinium). The nuclear apparatus is situated at the side which we have designated as the primary nuclear side. It is obvious that this designation is a relative one, and means the primary side within the limits of the family Ophryoscolecidae. We do not know whether the ancestors of Entodinium have undergone a torsion in the process of their evolution, but it is highly probable that they have.

In the Diplodiniinae the nuclear apparatus and the contractile vacuoles became shifted clockwise across the left ("right") body-side. The shift of the macronucleus in different genera of this subfamily ranged from about 100° (in Diplodinium s. str.) to 180° (in Ostracodinium), the development of the skeleton being directly proportional to the grade of torsion. The metoral membranelle zone remained approximately in the same transverse plane as the adoral zone. Only in Enoploplastron the metoral zone is slightly shifted caudad -- a trend which becomes prominent in the evolution of the subfamily Ophryoscolecinae. The third subfamily -- the Ophryoscolecinae -- is characterized by a high degree of torsion, considerable development of the skeleton and of the caudal spination, and -- before all -- by the elongation of the interzonal (or in Dogiel's terms -- prezonal) part of the body. Whereas in the Diplodiniinae the highest degree of torsion takes place near the middle of the body (the equator), in the Ophryoscolecinae it is the anterior -- interzonal -- part of the body which undergoes maximal twisting. The nuclear apparatus, which in this subfamily is situated caudad to the zone of maximal twisting is -- at least in the primitive genera of this subfamily -- displaced clockwise less than 180°.

It can be surmized, that the Ophryoscolecinae branched off from Diplodiniinae after the development of a fairly complex skeleton, but before the macronucleus had been pressed between the vacuoles, i.e. before the advent of the genus _Metadinium_. In contradiction to this suggestion is, however, the fact, that already the genus _Epidinium_ -- one of the primitive genera of the Ophryoscolecinae -- has a skeleton composed of three plates, closely resembling that of _Enoploplastron triloricatum_ (Dogiel 1925), which Dogiel placed in the genus _Ostracodinium_. It is possible, therefore, that the Ophryoscolecinae branched off from the Diplodiniinae later than is shown in Plate 1.

The subfamily Polydiniinae Kofoid 1935 is closely related to, and probably originated from, the Ophryoscolecinae. It is characterized by a very high degree of torsion, far exceeding 180° -- which is the maximal torsion observed in the Diplodiniinae. Both the genera of Polydiniinae inhabit the colon of the Indian elephant, thus differing from members of the previous three subfamilies, which are basically parasites of ruminants.

In Plate 1 (drawn at a magnification of x200), the genera are represented by species approximating the average size of species of the given genus. The plate shows clearly the increase in the average body-size of the Ophryoscolecidae in the course of their evolution. However, the largest sizes are attained not by representatives of the genera with the most complex organisation, but by species of Eremoplastron and Metadinium -- both comparatively primitive genera of Diplodiniinae (cf. Dogiel 1927, p. 26). Dogiel (1927) surmised that the increase in size of the Ophryoscolecidae in the course of their evolution is determined by their parasitic way of life. This, however, does not explain the difference in body-sizes in different subfamilies of the Ophryoscolecidae. Later Dogiel (1951) pointed out, that the rumen can be compared in its volume with the volume of a small natural water-basin, and that the Ophryoscolecidae thus live under conditions similar to those of free-living organisms, except that in the hostal environment food is more abundant. It might be surmised, that the increase in size of the Ophryoscolecidae in the course of evolution represents a particular case of the law of increase of size in phyletic branches of Cope-Depéret. However, this law was established by Cope on the basis of studies of evolution of vertebrates, and its inapplicability to the evolution of at least several branches of Protozoa was pointed out already by Depéret (1909). It is probable, that the differences in the increase in body-size in the evolution of the different branches of the Ophryoscolecidae depend on differences in food-habits. Whereas the increase in size may be of survival value for cellulose-feeders and predators, it may be of no advantage to bacteria- or starch-feeders. This would explain the large body-sizes attained by some genera of Diplodiniinae -- which are predominantly cellulose-feeders -- and the moderate sizes of the Ophryoscolecinae, which are basically starch-feeders.

Another remarkable character of the evolution of the Ophryoscolecidae is the dependence of the development of the caudal spination on the degree of torsion of the nuclear apparatus. Only primitive genera of the Diplodiniinae with nuclear apparatus situated at a considerable distance from the secondary nuclear side ("dorsal side"), e.g. *Diplodinium* and to a lesser degree *Eremoplastron*, have species with well-developed caudal spination. Genera with nuclei near the secondary nuclear side ("dorsal side") -- e.g. *Metadinium*, *Diploplastron*, *Polyplastron* and *Elytroplastron*--have no armed species, or, as in *Ostracodinium*, have only a few species with poorly developed spination. A similar regularity exists in the subfamily Ophryoscolecinae: genera with the nuclear apparatus near the middle of the left ("right") side of the body -- Epidinium and Ophryoscolex -- have well developed caudal spination, whereas genera which have undergone further torsion -- Caloscolex, Opisthotrichum, as well as the Polydiniinae -- have a poorly developed caudal spination.

Torsion is the basic factor in the evolution of the Ophryoscolecidae, determining the most important morphological features of this family. As a result of torsion the nuclear apparatus is displaced in the course of evolution of the higher Ophryoscolecidae and shifts from 100° to 180° across the body-side. Using the conventional designation "dorsal side" for the nuclear side of Entodinium -- the primary nuclear side -- we have to state, that in the course of evolution of the higher Ophryoscolecidae the nuclear apparatus and the contractile vacuole were shifted from the dorsal side to the ventral. Higher Ophryoscolecidae -- Diplodiniinae and Ophryoscolecinae -- can be united in the group Ventronucleata and opposed to the primitive group Dorsonucleata, comprizing only one subfamily -- the Entodiniinae. Leaving aside the Polydiniinae, possessing a high degree of torsion, we can affirm that in all Ophryoscolecidae -- higher as well as lower -- the macronucleus is situated dorsally to the micronucleus -- a character which helps to distinguish Dorsonucleata from Ventronucleata at first glance. These relations change and the structures become much more complicated when the torsion exceeds 180°, as the case is in Polydiniinae.

From this standpoint it would be interesting to study the morphology of other ciliates, and in the first place -- of other groups of Entodiniomorpha. A detailed study of the genera Spirodinium, Cochliotoxum and Tetratoxum of the Cycloposthiidae should probably throw new light on the origin of this most interesting family and on its relations to the Ophryoscolecidae.

5. Some Conjectures and Problems

On comparing morphological characters of Entodinium with those of the higher Ophryoscolecidae we have traced the torsional displacement of structures -- the contractile vacuoles, the left lateral groove and the nuclear apparatus -- in the course of their phylogeny. We do not know the causes of these processes -- as we do not know the causes of so many phylogenetic phenomena. However, it is hard to resist the temptation to put forward some hypothetical explanations. Trying to analyze the dynamics of the displacement of structures in the phylogeny of the Ophryoscolecidae, it is natural to regard it, to use Thompson's (1942) words, "as related to or resulting from the physical causes inherent in the entire system of forces to which the whole has been exposed, and under whose influence it has come into being". Already a superficial study of the mode of life of these ciliates reveals the remarkable fact that they swim in rotating clockwise, whereas the structures are displaced counterclockwise. Their displacement can thus be described as the lagging of these structures behind the rotation of the body. This displacement was extremely slow -- the transformation of ancestral Entodinium into Diplodinium may have necessitated a time-span of the order of a geologic period.

The occurrence of repeated torsions and detorsions in the life cycle of apostomatous ciliates, resulting in coiling and uncoiling of the ciliature, was studied by Walton and Lwoff (1935) and Lwoff (1950). A temporary displacement of structures in individual trichomonades and devescovinid flagellates was described by Kirby. In *Devescovina lemniscata* he observed "the rotation of entire system of organelles in a counterclockwise direction as viewed from the rear" (Kirby 1941, p. 62). In *Macrotrichonympha restis* "The axostyle, parabasal body, and nucleus moved as a unit, the relative position of these parts undergoing no alteration" (Kirby 1942, p. 127). These phenomena of short duration occurring in flagellates with semi-fluid nude cytoplasm are but slightly reminiscent of the phylogenetic phenomena in the Ophryoscolecidae -- ciliates invested with a fairly resistant pellicle and having a constant body-shape. We may conjecture, however, that the displacement of structures in the phylogeny of the Ophryoscolecidae in some way depends on their way of locomotion. The probable influence of such factors as the friction and the viscosity of the medium, the specific gravity of the nuclear apparatus and the centrifugal force developed in the course of locomotion, the precise character of this locomotion, and that of the body-shape -- will probably have to be taken into account. The role of persistence of characters, produced in these ciliates by *persisting* environmental factors has to be considered. Trying to analyze the dependence of displacement of structures in the phylogeny of the Ophryoscolecidae on their mode of life, we are forced to resort to vague hypothesis, bordering on guesswork. At this point it is safer to stop and to say "ignoramus", but not "ignorabimus".

SUMMARY

1. Examination of the rumen-faunules of domestic ruminants, collected in the Punjab, revealed a new species of *Entodinium* -- *E. simulans* sp. n. -- which produces sets of forms ("*caudatum*", "*loboso-spinosum*", and "*dubardi*") paralleling those of *E. caudatum* Stein.
2. A similar and hitherto unknown variability was found in *E. rectangulatum* Kofoid and MacLennan.
3. It is shown, that in the literature the specific names of *E. caudatum*, *E. loboso-spinosum* and *E. dubardi* were hitherto applied to parallel forms with a common type of caudal spination, belonging to at least three different species of *Entodinium*.
4. *E. simplex* Dogiel 1925 is regarded as a synonym of *E. dubardi* Buisson 1923.
5. It is shown, that within the "*caudatum*-*laterale*" group of *Entodinium* exists an evolutionary trend to the transformation of the left lateral groove into a narrow furrow and to a ventrad displacement of structures across the left body-side.
6. An unorthodox comparison of the left body-side of *E. simulans* sp. n. with the "right" body-side of *Diplodinium* s. str. resulted in the discovery of the role of torsional displacement of structures in the origin of the higher Ophryoscolecidae.

7. This new conception implies 1) the homologization of the right dorsal furrow of *Diplodinium* s. str. with the left lateral groove of *Entodinium* of the "*caudatum-laterale*" group, and 2) the homologization of the dorsal side of the higher Ophryoscolecidae with the ventral side of *Entodinium*.
8. The term "dorsal side", transferred from the morphology of higher animals into that of the Ophryoscolecidae, implied the constancy of the side termed "dorsal", and interfered with the discovery of the displacement of structures in their phylogeny, which is obvious for an unbiased observer.
9. A comparative study of essential generic characters of the Ophryoscolecidae has shown, that the torsional displacement of structures was operative in the phylogeny of all genera of this family.
10. The phylogeny of the Ophryoscolecidae is reconstructed on the basis of the new conception of their comparative morphology.
11. Three new subfamilies are established within the family Ophryoscolecidae: the Entodiniinae, the Diplodiniinae and the Ophryoscolecinae.
12. The Diplodiniinae and the Ophryoscolecinae are united into the group Ventronucleata and opposed to the primitive group Dorsonucleata which includes only one subfamily -- the Entodiniinae.

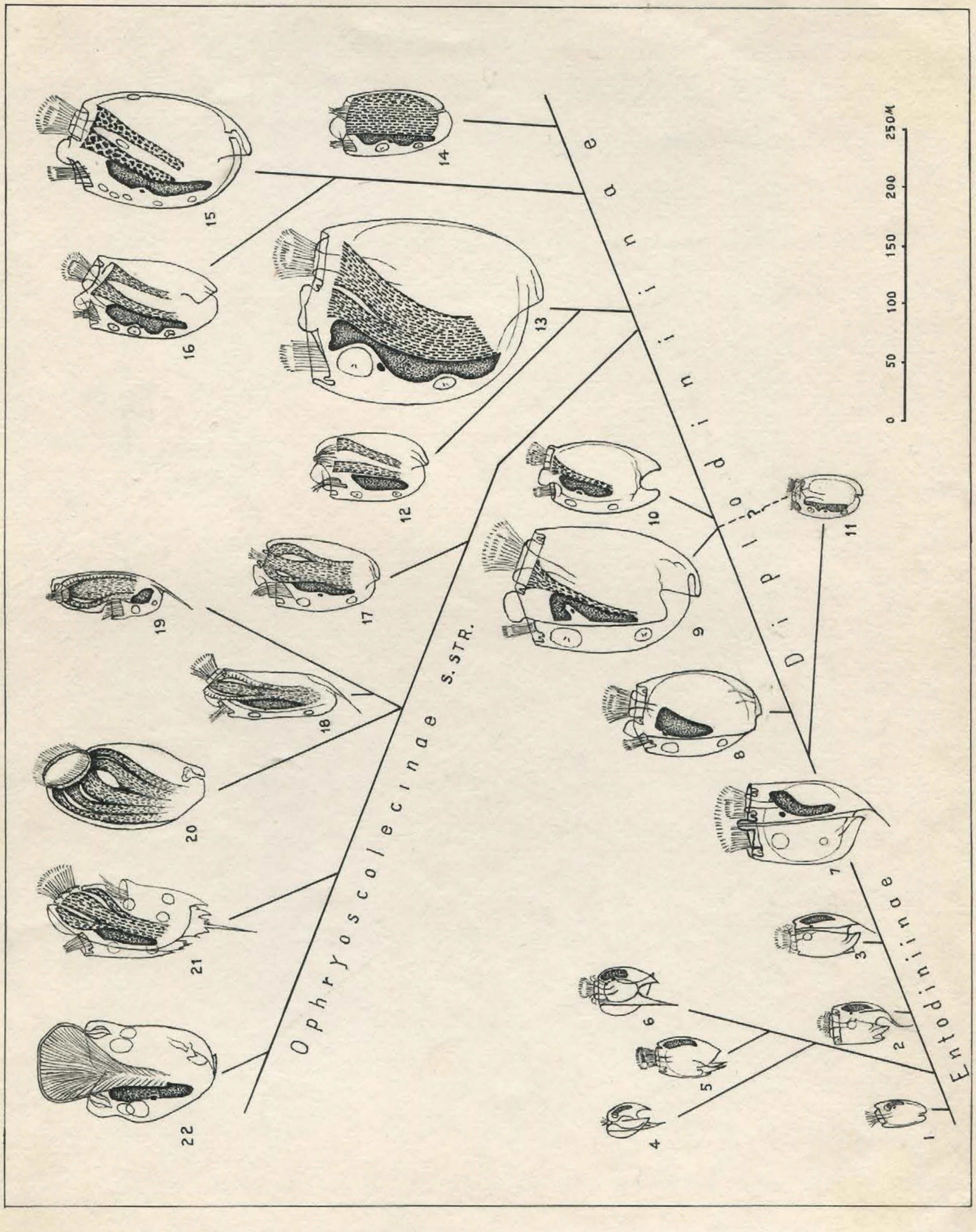
13. It is suggested that the torsional displacement of structures might have been operative in the phylogeny of the related family Cycloposthiidae.

14. An attempt is made to correlate the torsional displacement of structures in the phylogeny of the Ophryoscolecidae with the mode of life of these ciliates.

PLATE 1

All figures drawn at x200. Fig. 11 adapted from Kofoid and MacLennan (1932), Figs. 19, 20 and 22 -- from Dogiel (1927). All other figures are camera lucida drawings of stained and mounted material, collected by the author in Rawalpindi, W. Pakistan, from the rumina of *Bubalus bubalus* (Figs. 4 to 6 and 14) and from those of domestic sheep and goats (all other figures).

Fig. 1 -- *Entodinium nanellum* Dogiel 1923.
Fig. 2 -- *E. rectangulatum* Kofoid and MacLennan 1930.
Fig. 3 -- *E. simulans* sp. n.
Fig. 4 -- *E. indicum* Kofoid and MacLennan 1930.
Fig. 5 -- *E. bifidum* (Dogiel 1927).
Fig. 6 -- *E. tricostatum* Kofoid and MacLennan 1930.
Fig. 7 -- Hypothetical ancestor of the higher Ophryoscolecidae.
Fig. 8 -- *Diplodinium laeve* Dogiel 1927.
Fig. 9 -- *Eudiplodinium maggii* (Fiorentini 1889).
Fig. 10 - *Eremoplastron dilobum* (Dogiel 1927).
Fig. 11 - *Eodinium lobatum* Kofoid and MacLennan 1932.
Fig. 12 - *Diploplastron affine* (Dogiel and Fedorowa 1925).
Fig. 13 - *Metadinium tauricum* (Dogiel and Fedorowa 1925).
Fig. 14 - *Ostracodinium gracile* (Dogiel 1925).
Fig. 15 - *Polyplastron multivesiculatum* (Dogiel and Fedorowa 1925).
Fig. 16 - *Elytroplastron bubali* (Dogiel 1928).
Fig. 17 - *Enoploplastron triloricatum* (Dogiel 1925).
Fig. 18 - *Epidinium caudatum* (Fiorentini 1889).
Fig. 19 - *Opisthotrichum janus* (Dogiel 1923).
Fig. 20 - *Epiplastron africanum* (Dogiel 1925).
Fig. 21 - *Ophryoscolex caudatus* Eberlein 1895.
Fig. 22 - *Caloscolex camelinus* Dogiel 1926.


Ophryoscolecinae S. STR.
Diplodiniinae
Entodiniinae
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2
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4
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16
17
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19
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21
22
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50
100
150
200
250µ

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