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ABSTRACT—The behavior of *Heterolepidoderma* sp. was studied with the same approach as those already used for many species of ciliates. The ethogram we drew comprehends both helicoidal swimming (n = 20, r = 52.5 ±12.2 µm, pitch = 512 ± 101 µm , $\vec{v}$ = 215 ± 43 µm/sec), periodically interrupted by irregular patterns changing the direction of the swimming of random angles and creeping on the substrate. The latter behavioral state, very common for the species we studied, occurs along tracks formed by successive elements (circular, C, *vs* linear segments, S) joined to each other by two kinds of reactions, which change their trajectory. The surprising similarities and the unexpected differences between the behavior of this gastrotrich and those of the ciliates already studied from this point of view are discussed, on the basis of the dimensional ranges and ecological niches shared by these two, definitely unrelated groups of organisms.

INTRODUCTION

The outstanding relevance of behavior to express the adaptive strategies of whichever behaving organism (in this sense we speak of "adaptive behavior") is such a self evident fact that it has been taken into account even by scientists dealing with the construction of robots, whose behavior must also be adaptive in order to maintain them within ranges of the external parameters without hindering their own functions (Cliff, 1991; Meyer and Guillot, 1990; McFarland, 1991).

This concept of adaptive behavior was applied successfully to the ciliated protozoa (Ricci, 1990) with an etho-ecological attitude (Ricci, 1992a) to focus on and investigate several aspects of their anti-intuitive adaptive biology (Ricci, 1996), on the basis of the concept of the ethogram (Eibl-Eibesfeldt, 1967; Ricci, 1989a) and after standardizing the proper protocol (Ricci, 1992b). The overall outcome of these studies led us not only to expand the knowledge of many phenomena already known and described from many points of view: conjugation (Ricci, 1981, 1982; Ricci *et al.*, 1987), the predation of *Litonotus lamella* (Ricci *et al.*, 1996; Ricci and Verni, 1988), but also to explore entirely new aspects of the biology of these organisms, thus identifying new adaptive strategies (Ricci, 1989b; Ricci *et al.*, 1989), new habitats (Ricci *et al.*, 1991) and new stimuli (Lueken *et al.*, 1996; Ricci and Erra, 1995; Ricci *et al.*, 1997).

To deepen further our understanding of the phenomenon "behavior of the ciliates", a comparative approach was chosen and the ethogram of a gastrotrich (*Heterolepidoderma* sp.) was drawn. This phylum was studied for two basic biological characters: (a) its dimensional range, almost completely overlapping that of ciliates: this implies that all of the selective, dimension-dependent pressures are shared by gastrotrichs and ciliates (cf., the Reynolds numbers are fairly similar for both of them); (b) the ciliary propulsion system, which is basically the same as for ciliates, while the muscles are used to contract the body and to bend it laterally. On the other hand, gastrotrichs are pseudocoelomate Metazoa, namely fairly complex, multicellular organisms with developed muscles, sensory organelles and a central nervous system. As far as the neuro-motor apparatus is concerned, the following things must be recalled. The nervous system is represented by a brain, composed of two ganglionic masses, connected dorsally by a commissure. The brain is directly connected to the sensory bristles (= modified cilia) and tufts of the head, which are believed to be tactile receptors. The nervous system is connected also to the three longitudinal pairs of ventral and lateral muscles, which are responsible for the differential contraction of the body. The motive force is given by the active ciliary beating. Their biology is already quite well known from many points of view (Balsamo, 1980, 1983; Barnes *et al.*, 1988; Beauchamp, 1965; Rieger, 1976; Rieger and Rieger, 1977). Could it be possible to find any basic similarities and/or differences between the behavioral patterns of these two groups of organisms, very different from the evolutionary point of view, but very close to each other (Luporini *et al.*, 1970, 1971; Papi, 1957) in terms of body dimensions, propelling engines (Hyman, 1951; Remane, 1936), habitats and ecological niches (Fenchel, 1987)? With all of these considerations in mind, the behavior of this phylum was analyzed. Specific data in this field is available in the literature only in Zelinka (1889) and merely receives the odd mention in the papers of other authors.

MATERIALS AND METHODS

Our specimens of *Heterolepidoderma* sp. were collected in a freshwater canal close to Pisa, in samples containing also many green unicellular algae, microflagellates, diatoms, ciliates and rotifers. Eigh-

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teen specimens were isolated, one per each depression of 6 three-depression slides, in their collection fluid: three days later several droplets of lettuce medium inoculated by *Enterobacter aerogenes* were added (Ricci *et al.*, 1980; Sonneborn, 1950, 1970). When the culture volumes were of 5–10 ml, they were passed into Petri dishes and kept in an incubator at 22°C.

The determination of the genus was made by Prof. Tongiorgi and Prof. Balsamo (University of Modena). To draw the ethogram, a standard experimental apparatus was set up, according to the basic technique described by Ricci (1989a). The TV recording sessions, the analysis of the tracks and the measurements of the different elements were carried out according to the same protocol, which must be consulted for a thorough discussion of the terminology and the concepts related to the matter. The data obtained were processed statistically by means of the standard STATGRAPHICS program: for the linear correlation of Fig. 2 the non parametric test of Spearman was used, while for the significance of the differences between groups of data the Kruskal-Wallis non parametric test was used.

RESULTS

The species, 84 μm long, can either swim or creep on the substrate. Before drawing the ethogram, a deep knowledge regarding with the behavior of the species was acquired, by means of daily handling, experiencing and culturing: after about 4 months, 20 tracks of swimming *Heterolepidoderma* sp. and 20 of creeping specimens were analyzed specifically to draw the ethogram.

The swimming

The normal forward swimming occurs along leftward helicoids, which develop around a straight central axis; the helicoids are periodically interrupted (every 6–7 sec) by behavioral reactions which lead the organism to change the swimming direction (Fig. 1A). The body of a swimming gastrotrich is C-shaped (due to a slightly asymmetric, ventral muscular contraction) and its ventral surface is kept constantly towards the central axis: the curve of the body identifies the
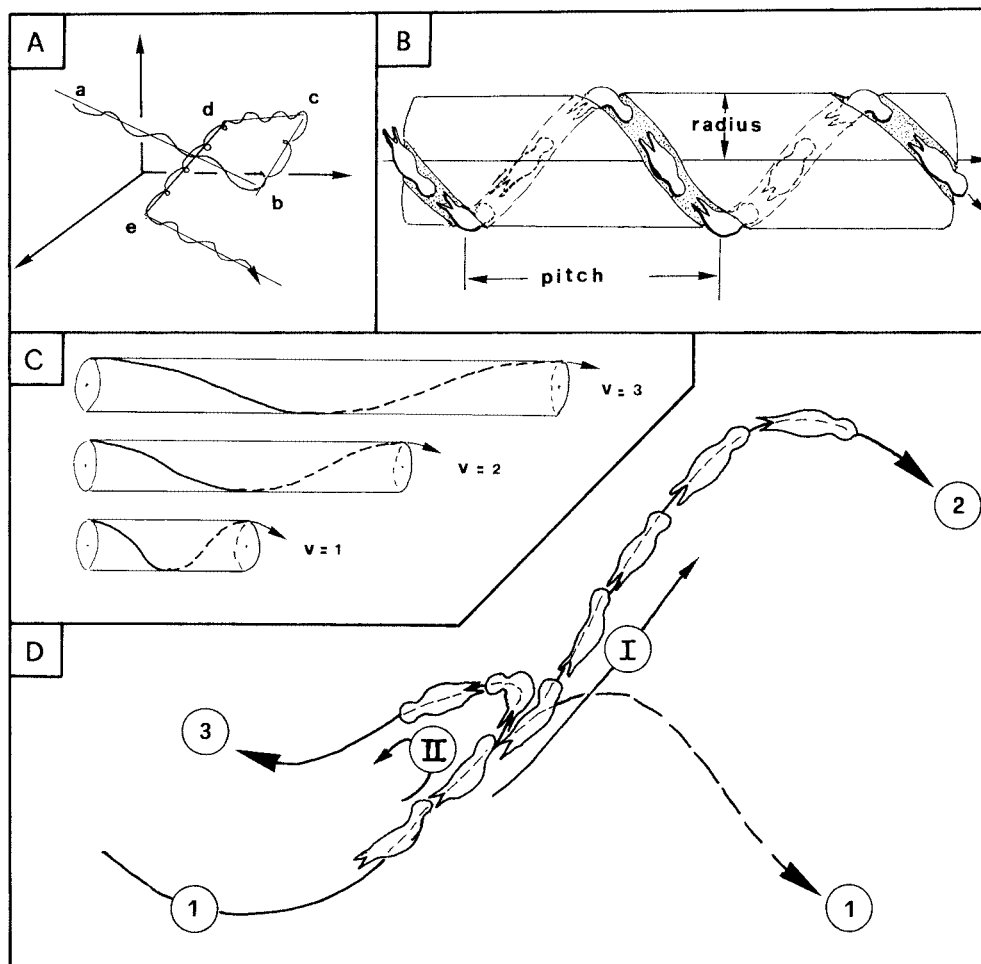

Fig. 1. The swimming of *Heterolepidoderma* sp. (**A**) the three dimensional scheme of a track, periodically interrupted in b, c, d, e. (**B**) the helicoidal path followed by a ventrally bent specimen; the radius and the pitch are indicated. (**C**) the pitch (but not the radius) changes with the swimming velocity. (**D**) the trajectory changes: I, the axis of swimming from 1 passes to 2; II, if the body is U-bent, the axis of the swimming passes from 1 to 3.

Table 1. The measurements of several parameters of the swimming of *Heterolepidoderma* sp. are given in the first column and are compared with the corresponding figures found in the literature for the different species of ciliates

Parameters	*Heterolepidoderma* (90 µm)	*Litonotus* (250 µm)	*Blepharisma* (300 µm)	*Oxytricha* (120 µm)	*Euplotes* (90 µm)	*Aspidisca* (70 µm)
Pitch (P) (µm)	512	565	981	220	425	24
Diameter (D) (µm)	105	80	148	80	86	18
P/D	5.2	7.06	6.6	2.75	4.95	1.3
Linear Velocity (Vl) (µm/s)	215	283	388	750	803	25
Helicoidal Velocity (Vh) (µm/s)	256	309	434	1139	951	64
Vl/Vh	1.19	0.91	1.1	1.5	1.2	2.6

helicoidal track itself which can be described geometrically by its radius, namely the distance between the track and the central axis of the helicoid (n = 20; x̄ = 52.5 ± 12.2 µm) and by its pitch, namely the distance between two points in phase (n = 20; x̄ = 512 ± 101 µm) (Fig. 1B).

The organisms swim forward at an average speed of 215 ± 43 µm/sec (n = 20): this is called linear velocity (V_l), it was measured along the straight axis of the helicoid to distinguish it from the true velocity (called helicoidal velocity, V_h) which is a little higher: 256 ± 41 µm/sec, n = 20. The time spent to cover a single pitch is fairly constant, namely 2.42 ± 0.40 sec (n = 20): it corresponds to the time requested to swim around the axis of 360°. This rotational velocity was quite constant, it is evident that different velocities along the helicoid make the pitch itself shorter or longer (Fig. 1C). Only more rarely, e.g. when *Heterolepidoderma* sp. approaches an environmental discontinuity, such as the substrate or the surface between air and water, does the species straighten its body and start swimming along straight trajectories for a short while.

Table 1 shows the ratios between pitch and diameter of the helicoid and between the linear and the helicoidal velocities, in comparison with the similar values for different ciliates (data calculated from the data available in the literature): none of these figures seems to distinguish the gastrotrichs from the species of ciliates so far studied. The helicoid was periodically interrupted by a peculiar reaction (Fig. 1D): the body bends longitudinally and asymmetrically, the bending itself determined the new direction of the swimming. In Fig. 1D, the first change of the swimming direction (I) is obtained by a short lasting straightening of the body: as a consequence, the 1-track is changed into the new 2-track. If the bending is very clear-cut, namely the caudal furca comes close to the head, the correction angle is of about 180°, as shown in the same figure. The II correction indeed leads the gastrotrich to shift from the 1- to the 3-track, namely in a direction approximately opposite to the previous one.

The creeping of *Heterolepidoderma* sp

The 20 tracks analyzed to draw the ethogram covered a total length of about 56,400 µm. The tracks are formed by different basic elements: the elements along which the organisms move for a certain period (the so called Long Lasting Elements, LLE) and those which mediate a change of trajec-

Table 2. The quantitative comparison between the S and C Long Lasting Elements

	N°	%	l (µm)	Δt (s)	v⃗ (µm/s)
S	108	57	169 ± 67	0.98 ± 0.25	170 ± 63
C	81	43	470 ± 191	3.85 ± 1.6	121 ± 56

tory and somehow connect a LLE to the next. These elements are relatively short in time and have been called the Short Lasting Elements (SLE). This terminology, as already mentioned in the Materials and Methods Section, comes from that defined for the ethogram of the ciliates by Ricci (1989a). The LLE can be described as circular elements, C (not geometric arcs) or linear segments (S). Table 2 describes their response percentage, average lengths, durations, together with their relative velocities: it shows that *Heterolepidoderma* sp. tends to prefer the S (three times over five, on average), along which it creeps for shorter spaces (169 µm vs 470 µm), for shorter length (about 0.98 sec vs 3.85 sec), at higher speeds (170 µm/sec vs 121 µm/sec) than it does along the C elements. The study of the single velocities along the tracks, moreover, indicates that each organism tends to use only a narrow range of velocities, among those observed for the whole population: in other words, the gastrotrichs clearly behave according to the individual morpho-physiological characteristics.

The close correlation found between the length of the organism and its velocity (p < 0.01) (Fig. 2), shows that the velocity increases by about 100 µm/sec for an increase of 10 µm in the body length. During its forward creeping along both the C and the S, the organism rhythmically moves laterally its anterior end (Fig. 3): when the velocity ranges around 1 Relative Unit (RU) (about 80–90 µm/sec) the oscillation is of 1/sec (Fig. 3A), while when the velocity is of 2 RU/sec (or more) the frequency decreases to about one oscillation every 2 sec, due to the occurrence of a short S between two successive oscillations (Fig. 3B). The overall pattern seems to indicate that the body flexibility of *Heterolepidoderma* sp. is used to scan regularly the environment using the sensory bristles in its cephalic part. Two types of trajectory changes (SLE) have been recognized. Type I SLE (Fig. 3D) consists of an oscillation of the cephalon, either to the right or to the left of the organism, wider than the normal ones, i.e. the angle between
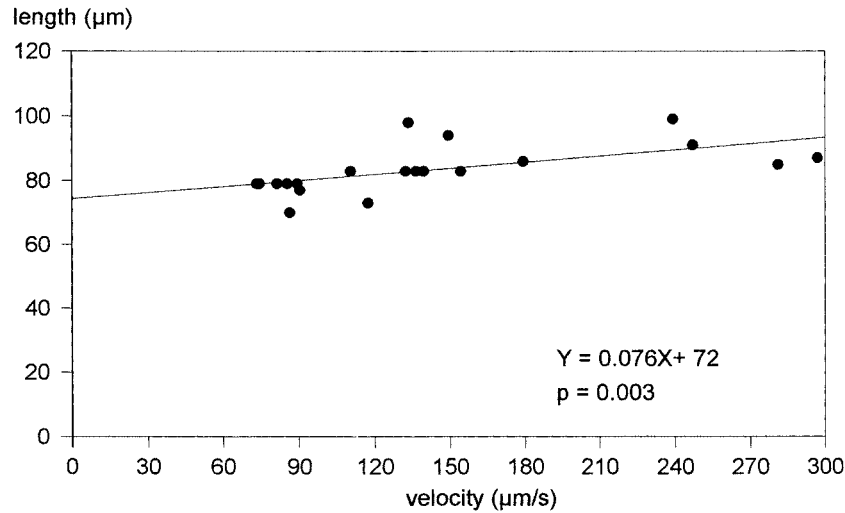
Fig. 2.   The significant linear correlation between velocity and body length.
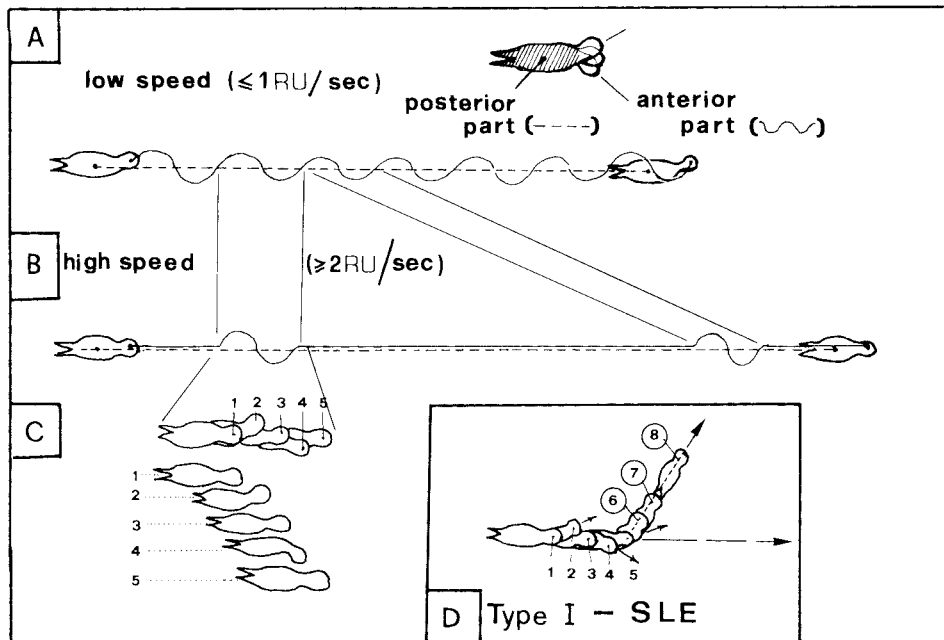

Fig. 3.   The creeping of *Heterolepidoderma* sp.. A: the low speed pattern. The anterior part of the body moves forwards along a sinusoid track, while the posterior part creeps in a straight line. B: the high speed pattern. The body is kept rigid for about 2 sec, the oscillations of the anterior part occurring only periodically, for about 1 sec and one RU. C: the lower left panel illustrates one oscillation period, roughly covering an RU. D: this panel schematically indicates the way type I SLE is performed; the body is bent to the left (in this case) of an angle roughly twice as wide as the normal oscillation angle (n. 6); the posterior part follows the anterior in the new direction (n. 7, 8).

the straight direction of the creeping and that of cephalon is wider than 60°. Once this occurs, the organism starts creeping in the new direction. Type II SLE (Fig. 4A) is performed whenever *Heterolepidoderma* sp. approaches an obstacle: a) it slows down to velocities ranging around 40–50 µm/sec (Fig. 4B, steps 2, 3, 4); b) it increases the frequency of the lateral scanning of its environment; c) it contacts the obstacle (Fig. 4B, step 5) and d) it shortens its body length by about 1/3; e)

it stops, anchoring the caudal furca to the substrate (Fig. 4B, steps 6, 7); f) it bends, either to the left or to the right, forming an angle as wide as $146 \pm 47°$ (n = 29) (Fig. 4B, step 8, 9); g) it detaches from the substrate and starts creeping forward at a progressively increasing velocity, until the normal values are attained again. The bending velocity (146° in 0.6 sec) can be expressed by an angular velocity $\omega \approx 243°/sec$.
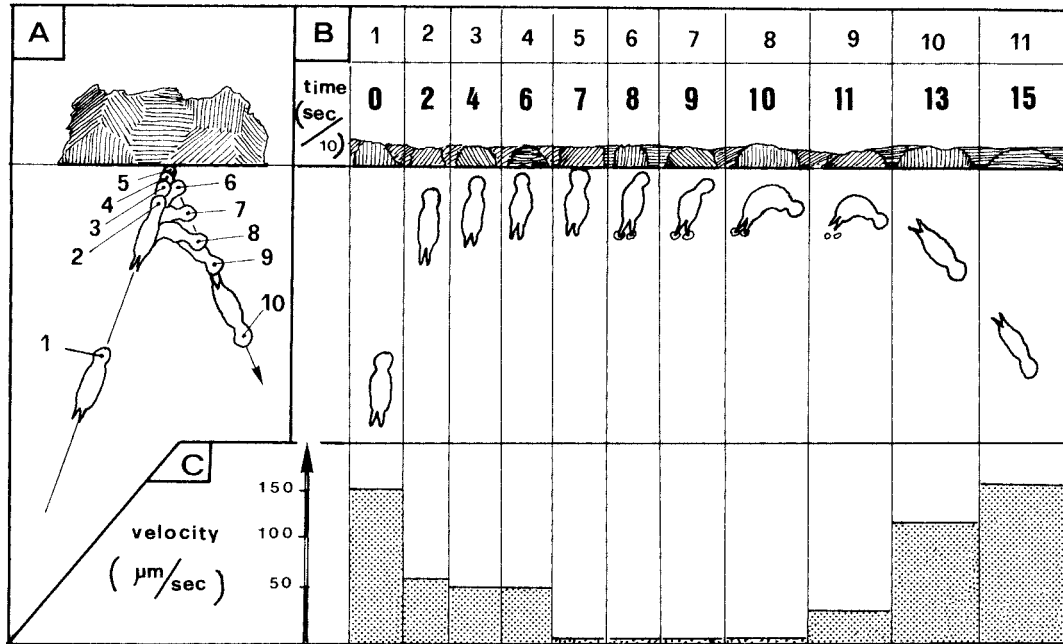
Fig. 4. A: type II SLE as drawn directly from the TV screen: 1) the creeping specimen; 2–10) the trajectory change. Shaded area indicates obstacle. B: the successive steps of the same reaction: 1–4) the forward creeping at a reduced speed; 5) the bump against the obstacle (shaded area); 6) the caudal furca adheres to the substrate; 7–8) the body is bent to the right (in this case); 9) the bending continues for a short while, also after the furca is detached from the substrate, to cover a total angle as wide as about 146°; 10–11) at this point the forward creeping in the new direction is resumed. Time (sec/10): the relative duration of the different steps of the reaction. C: for the sake of clarity, the approximate velocities of the gastrotrich at the different steps are indicated by the height of the bars.

DISCUSSION

This paper represents the first report specifically dedicated to the study of the behavior of the gastrotrichs, previous data on the topic being available only as a sort of by-product in papers more specifically dealing with the biology of these organisms in general (Remane, 1936; Zelinka, 1889). The outcome of this research describes several traits in the behavior of the gastrotrichs which clearly reflect their multicellular nature and their complexity as far as the sensory, the nervous and the locomotion apparati are concerned. Among these, the Circular LLE are very paradigmatic, due to a continuous change in both the centre and in the radius of their otherwise circular trajectories. This trait is likely related to the kind of ciliature of these organisms (distributed among many ciliated, singly innervated epithelial cells, which are capable of continuous, differential modulations of their activity). This trait, coupled with a flexible body, clearly distinguishes the gastrotrichs from the ciliates, at least as far as the species already studied are concerned (Ricci, 1990); these eukaryotic unicells are known to control their ciliary propellers by modulating their single membrane potentials (Machemer, 1974; Machemer and Deitmer, 1987; Machemer and Teunis, 1996), in much the same way as *Amoeba* does (Soyers *et al.*, 1979). The fact that they are one piece-one body organisms seems to account for the fact that they actually creep along geometrically perfect arcs (either leftwards A−, or rightwards A+), thus behaving according to successive, different "quantic" patterns, each being observable as a LLE (A−, A+, S) (Ricci, 1996).

The gastrotrichs, moreover, seem to behave according to several patterns clearly related to and depending upon basic structural factors. The C-shaped body, for instance, determines not only the swimming direction and pattern, but also the dimensions themselves of the basic swimming unit (pitch and radius, Fig. 1B). The close correlation between the body length and the creeping velocity, on one hand (Fig. 2), and the oscillation period and space (1 RU/sec) of the creeping (Fig. 3) on the other, are two clear examples of the same clear correlation between morphology and behavior. No correlation of this kind has ever been reported for the ciliates so far studied from this point of view.

Beyond these characteristics apparently typical of the gastrotrichs, several other behavioral traits are shared by them and by the ciliates: a) the helicoidal swimming; b) the order of magnitude of the ratio between the pitch and the diameter of the helicoidal unit; c) the creeping tracks formed by successions of alternated LLE and SLE; d) the clearcut individuality of the quantitative parameters of the singular behavior. These behavioral patterns the gastrotrichs share with the ciliates might be envisaged as the results of adaptive convergences, which are presumed to be quite strong, due to the dimensional ranges, habitats and niches shared by these two groups. The helicoidal swimming of the C-shaped gastrotrichs was also reported by Remane (1936), who apparently disregarded

the straight swimming and the basic problem underlying it: how can a gastrotrich perceive the obstacle from a distance? The description of the type II SLE (Fig. 4) strengthens the importance of this aspect of the biology of *Heterolepidoderma* sp.: how can it slow down its own locomotion in the proximity of an obstacle? The changes in swimming/creeping direction, triggered by the body bending (cf. also Zelinka, 1889), controlled by the CNS, are very interesting because they differ from those described for the ciliates studied for their behavior so far (Ricci, 1990; Ricci *et al.*, 1995). The multicellular organization of the gastrotrichs (Teuchert, 1974, 1977, 1978) enables them to show a whole wide range of graded behavioral responses, quite different from that reported for the ciliates, one piece-one body organisms evidently far simpler than the gastrotrichs (Fenchel, 1987; Sleigh, 1989). The laterally oscillating behavior, carried out during the forward creeping, seems a clearly adaptive one. Just by acquiring a periodical, modulable oscillation, these small animals make a significant jump in their environmental scanning potentialities, closely related to the sensory organelles of their cephalic region (Balsamo, 1983; Beauchamp, 1965). On this point, the C- and the S- LLE can be considered as two patterns definitely differing from each other not only due to their geometry (circular vs straight) but rather because of their possible adaptive significance. The C elements ($\approx$ lower speed) may be expected to express the exploring phase of the locomotion, while the S elements ($\approx$ higher speed) should represent the transferring tracts.

The present study on the behavior of *Heterolepidoderma* sp. is a first contribution to the understanding of the possible relationships between gastrotrichs and ciliates and some adaptive behavioral traits possibly shared by these two other groups have been identified. To analyze the problem further, two other groups are currently being studied in our Lab to draw their ethogram: A) a flexible ciliate, *Lachrymaria*, to investigate the possible contribution of a non-rigid body to the general behavior of these organisms; B) *Xenotrichula* sp., a gastrotrich with cirri, namely the motor organelles each formed by many cilia adhering to each other longitudinally and working as a unique "limb" (Ricci, 1989a). The cirri, characterizing the group of the Hypotrichs, are believed to represent the upper limit of the ciliary propulsion, as far as the structural/functional complexity is concerned. The study of the behavior of *Xenotrichula* is expected to deepen our understanding of the evolutionary significance of this kind of organelle for the adaptive behavior of a species.

ACKNOWLEDGMENTS

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