from day to day and no sudden offsets appeared in the data, as was reported, for example, for a broken cable off the coast of Florida used for ocean transport studies (*15*). A potential drop less than about 0.5 V might be expected between the iron and copper electrodes (*16*). Such an electrochemical potential would not alter the basic conclusion that the natural potential drop measured in the experiment was near zero, so that the results in Fig. 3A are representative. For example, the voltages expected for values of $E(c)$ ranging over a factor of about 40 around the measured value for $N_n = 1$ are plotted in Fig. 3B. For reasonable estimates of $\sigma(c)$ of about 10^2 to 10^3 S/m, values of the toroidal magnetic field are still of the order of 10^{-5} to 10^{-3} T (Fig. 3B).

Steady ocean currents that do not complete a closed circuit loop across the length of a cable, such as tidal components with periods greater than the time interval of data, could produce a potential drop across the cable that would mimic a d-c potential over the time interval of analysis. However, analysis of the data for the entire time interval, as well as for five separate days within the total interval, revealed similar, small potentials within the calculated variances (Table 1). Furthermore, the spectrum estimation procedure has sufficient resolution to isolate all but the low-amplitude monthly lunar and semiannual solar tides (*17*). Extrapolating from the K_1, K_2, and S_2 tidal amplitudes in the data, the lunar and solar tides should not appreciably influence the d-c estimate.

The measured electric field from this experiment places some severe constraints on the toroidal field magnitude at the core-mantle boundary, if values of the lower mantle conductivity [10^2 to 10^3 S/m (*18*)] inferred from analyses of the secular variation are used. This would suggest a toroidal field at $r = c$ of about 10^{-4} to 10^{-3} T, which is comparable to the poloidal field.

A complicating matter in alternative attempts to arrive at values of σ in the lower mantle is the sudden ("impulse") changes in the geomagnetic secular variation (*19*). Although a straightforward interpretation of a change with a 2- to 4-year period would imply a low conductivity ($\sim 10^2$ S/m) at the core-mantle boundary, treating the mantle as a filter is not inconsistent with a value for $\sigma(c)$ of approximately 10^2 to 10^3 S/m (*20*). Interpreting such a geomagnetic impulse as a purely internal process (in contrast to external processes, such as solar cycle–dependent geomagnetic activity) has been called into some question (*21*).

On the basis of the work of Roberts and Lowes (*14*) and assuming that the conductivity at the core-mantle boundary is of the order of 10^2 to 10^3 S/m, our result for the large-scale d-c potential is consistent with the toroidal and poloidal fields being of approximately the same magnitude at $r = c$. However, a theoretical complication may exist in that Backus has recently used a singular perturbation method for estimating the electric field produced in the mantle by the core dynamo (*22*). Backus shows that, assuming that the conductivity has only one local minimum in the mantle, the resulting critical layer will screen out any internal-origin electric field except for the case where the critical layer occurs at the earth's surface. A null result, such as that obtained here, would be consistent with such a model. Further work is required to investigate the validity of such model considerations.

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A Unique Symbiosis in the Gut of Tropical Herbivorous Surgeonfish (Acanthuridae: Teleostei) from the Red Sea

Abstract. *Herbivorous surgeonfish (*Acanthurus *species) in the Red Sea harbor gut symbionts that include bacteria, trichomonadid flagellates, and a peculiar putative protist that attains densities of 20,000 to 100,000 cells per milliliter of gut contents. The structure, mode of reproduction, and within-gut distribution of the latter are described. This may be the first report of an organism of this type and the first evidence of a consistent endosymbiosis in the gut of a herbivorous marine fish.*

Lev Fishelson
Department of Zoology,
Tel Aviv University,
Ramat Aviv, Tel Aviv, Israel
W. Linn Montgomery
Department of Biological Sciences,
Northern Arizona University,
Flagstaff 86011
Arthur A. Myrberg, Jr.
Rosenstiel School of Marine and
Atmospheric Sciences, University of
Miami, Miami, Florida 33149

Symbiotic relations between organisms are often the products of coevolutionary processes (*1*), may exhibit close interactions on ecological, anatomical, physiological, or biochemical levels, and involve a broad array of taxa (*2–4*). In most instances of gut endosymbiosis involving herbivorous organisms, the gut flora and fauna either participate in the digestion of plant material on which the host feeds or provide important micronutrients to the host (*3, 4*).

Such well-defined symbiotic relations have not been described for marine fish. Although obligate anaerobic bacteria from freshwater fish have been recorded (*5*), studies of gut microfloras and faunas of fish leave the impression that there are few obligate relations of this sort and that gut microbes often reflect microbial populations in the water or the food. Furthermore, most studies have been performed on carnivorous or omnivorous fish and have generally overlooked the possible role of gut microbes in herbivorous marine species that rely on refractory and biochemically complex nutrients from macroalgae (*5*, *6*). Our discovery of a unique assemblage of organisms inhabiting sections of the gut of a surgeonfish appears to represent the first case of well-defined endosymbiosis between unicellular organisms and herbivorous marine fish.

While working on the ecology and biology of surgeonfish (Acanthuridae) near Eilat, Israel (Gulf of Aqaba, Red Sea), during 1982 and 1983, we found that the gut of *Acanthurus nigrofuscus* is densely populated by unicellular prokaryotic and eukaryotic microbes (*7*), including bacteria, especially bipolar flagellated *Spirillum* species; flagellates, with a dominance of trichomonadids; and a peculiar cigar-shaped organism (Fig. 1a) that apparently does not fit into any current classification of the Protista. Although even the higher taxonomic position of the latter organism remains unclear, several features suggest that it is a protist, and we will refer to it as such here.

The protist was gigantic compared to other gut microbes in *A. nigrofuscus*, ranging in length from approximately 30 to 500 μm (Fig. 2a), although individuals exceeding 200 μm accounted for less than 15 percent of the population. Average maximum width was 13.8 percent (standard deviation, 4.0 percent; $n = 20$) of length, or approximately 5 to 45 μm for the more common size classes.

The surface of the protist was uniformly covered by delicate, hairlike structures (Fig. 1b) that appeared to be 70 to 150 Å in diameter—much less than expected for typical cilia and flagella. Under the light microscope beatings of this layer of filaments were visible, although the individual structures were not. Transmission electron microscopy failed to reveal the typical 9 + 2 microtubular structure of cilia and flagella. However, the locomotion of the live organism resembled patterns observed in ciliates: the protists moved rapidly back and forth, spiraling around the long axes of their bodies.

During locomotion the organism's cigar-like shape did not change, suggesting the existence of a rigid pellicle or cortex. Measurements of the cortex in cross section with a light microscope indicated a thickness of 1.5 to 3.5 μm. No other external features were evident, not even anything resembling a mouth.

A large, oval to elongate nucleus, 48 to 60 μm long and 5 to 10 μm wide, was

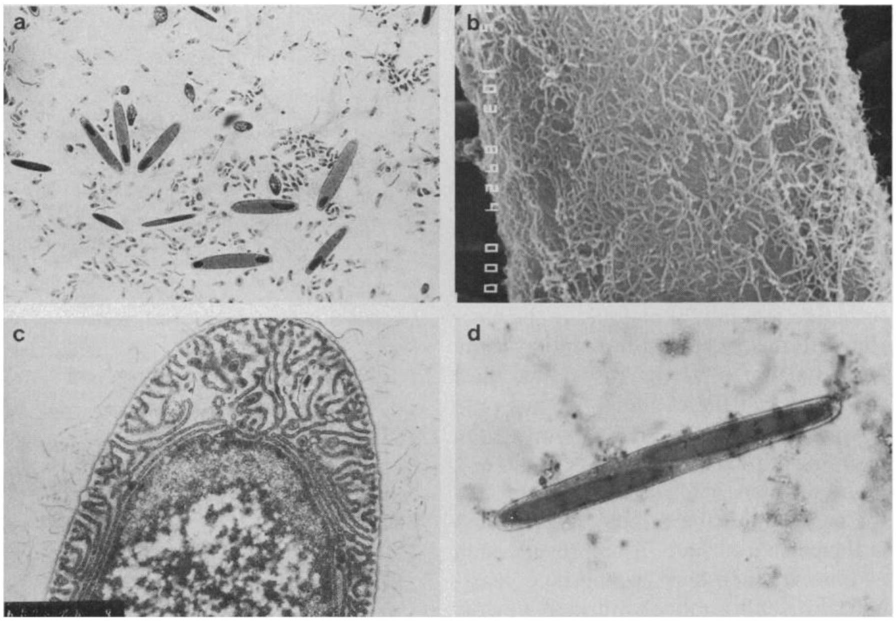

Fig. 1. (a) Intestinal contents of *A. nigrofuscus*, showing predominant microorganisms: serpentine *Spirillum*, ovoid trichomonadid flagellates, and the cigar-like putative protists. Stain, hematoxylin and methylene blue; magnification, ×400. (b) Scanning electron micrograph of a protist's surface. The organism is approximately 7.3 μm wide. Magnification, ×1400. (c) Transmission electron micrograph of a longitudinal section through the protist, showing the large nucleus and elaborate tubular system. Magnification, ×18,000. (d) Duplicate daughter cells within the maternal cortex. Magnification, ×40.

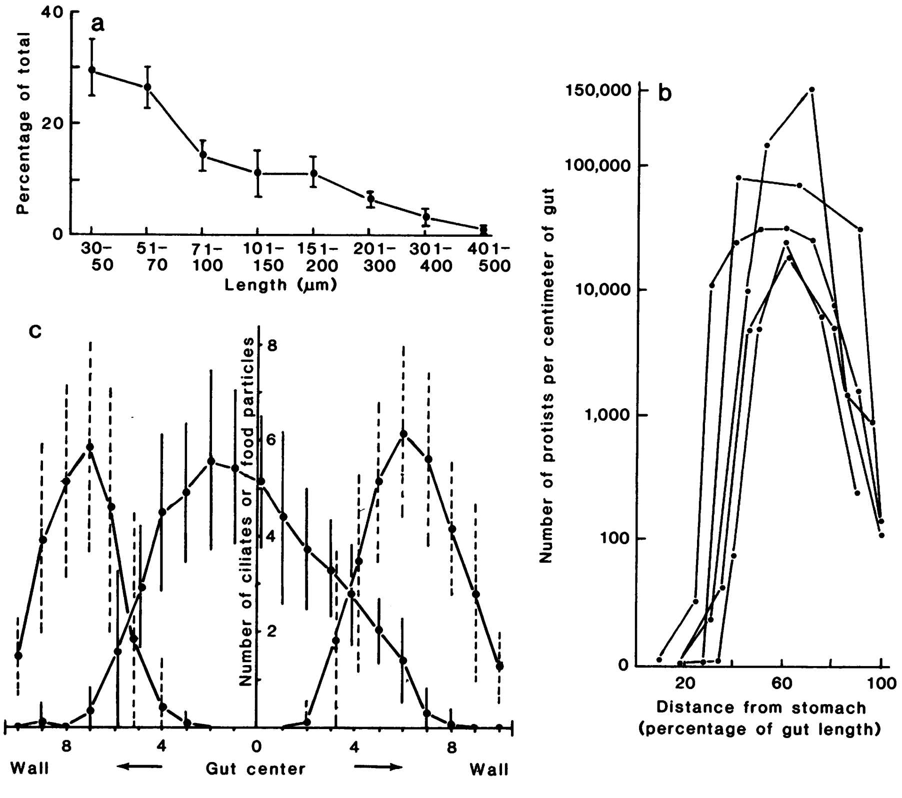

Fig. 2. (a) Frequency distribution of lengths of protists from the gut of *A. nigrofuscus*. Samples were pooled from various sections of the intestines of five fish and a frequency distribution was determined for each fish. No attempt was made to assess local differences in length distributions. Approximately 20,000 protists were measured. Error bars represent ±1 standard deviation from the mean of each category for five individual fish. (b) Distribution of the protist along the intestine. Each line represents the distribution for an individual fish. Distance along the gut was measured immediately posterior to the pyloric cecum. (c) Counts of protists (dashed error bars) and food particles (continuous error bars) in microscope transects across the middle of gut cross sections. Twenty sections were analyzed from ten fish with a Visopan microscope. Error bars represent ±1 standard deviation from the mean for the 20 sections.

visible at one end of the organism. In some individuals two nuclei were present, one at each end; they ranged from 80 to 125 μm in length. Only one other intracellular organelle was clearly identified: an elaborate tubular network situated between the nuclear membrane and the peripheral ectoplasm (Fig. 1c). Centrally located tubules tended to run parallel when they were close to the edge of the nucleus; more distally, they branched and eventually ran perpendicular to the plasma membrane. Micronuclei, mitochondria, ribosomes, or distinct endoplasmic reticulum were not evident in the sections we prepared.

As mentioned above, two nuclei of similar size were visible in some individuals. We believe that this is a stage in the reproductive cycle. From observations of many cells we identified a sequence of development that begins with duplication and growth of nuclei, continues with development of two daughter cells within the cortex (Fig. 1d), and ends with the emergence of these cells through a centrally located, oblong split in the envelope. In many cases the two daughter cells emerge simultaneously, leaving behind the empty maternal cortex. As far as we know, this mode of reproduction has not been described for other protists (*8*).

The protist showed a distinct pattern of distribution along the gut of *A. nigrofuscus*. It was absent from the stomach and rare in the foremost portion of the intestine (Fig. 2b). Densities rose dramatically beyond the first 30 percent of the intestine's length behind the stomach, were maximal at 40 to 60 percent of gut length, and dropped precipitously in the posterior 20 percent. The highest number estimated per centimeter of gut length (representing a volume of 0.3 to 0.5 ml) was more than 100,000. The highest densities were observed in a section immediately posterior to a sharp U-turn in the intestine, but there are no distinctive changes in the anatomy of the posterior gut, where numbers declined. In addition, larger individuals tended to occur in greater frequency in the anterior and middle portions of the intestine, while small individuals prevailed posteriorly. The larger organisms also exhibited the greatest frequency of doubled nuclei and emerging daughter cells. In a cross section of the gut (Fig. 2c), protists are seen in greatest numbers next to the gut lining and are not mixed within the centrally located bolus of algae.

This protist is a very predictable element of the gut fauna of *A. nigrofuscus* in the northern Red Sea. We recorded it from each of several hundred specimens collected from the Eilat area during all seasons. In addition, fish of the same species collected from several locations around the Sinai Peninsula (Râs Burka, Râs Nusrâni, and Râs Garra) also contained the symbiont; these sites span more than 400 km of coastline.

The protist was also found in preserved specimens of *Acanthurus sohal* collected at Râs Garra, Gulf of Suez, but was absent from the guts of other members of the same fish family, specifically *Ctenochaetus striatus*, *Zebrasoma xanthurum*, and *Zebrasoma veliferum* from the Gulf of Aqaba and *Acanthurus glaucoparieus* and *Prionurus punctatus* from the Gulf of California, Mexico. It was also absent from the rabbitfish *Siganus luridus* (Siganidae), a herbivore that feeds on the same foods over the same substrates and sometimes within the same groups as *A. nigrofuscus* at Eilat. Furthermore, it has not been recorded from other species of *Siganus* in the Red Sea (*9*).

Assuming that infection occurs through the mouth, this pattern of occurrence may be related to the anatomy and function of the surgeonfish stomach. Any gut action that would damage or destroy the symbiont would interfere with its establishment in the intestine. As with many other species of surgeonfish (*10*), *C. striatus*, *P. punctatus*, and, to a lesser degree, species of *Zebrasoma* have a thick-walled, muscular stomach that serves a grinding function much like that of the avian gizzard. This type of stomach is lacking in *A. nigrofuscus*, *A. sohal*, and *A. glaucoparieus*.

What is the pathway of infection or reinfection? Seven infected specimens of *A. nigrofuscus* that were starved for 2 to 3 days became protist-free, so emptying of the gut may lead to rapid loss of the organism. *Acanthurus nigrofuscus* follows a pattern typical of tropical herbivorous fish in restricting its feeding to daylight hours and resting in reef crevices at night. We discovered, however, that they retain a large bolus of incompletely digested food containing the protist in the posterior intestine overnight. Thus they do not completely void the gut contents at night. At the onset of feeding the next morning, the fish expel the undigested algae over the beds of subtidal turf algae on which they feed each day. This dispersal of symbiont-laden feces over the algae cover may provide the means by which the fish become infected or reinfected by their symbionts.

Several features of the protist's distribution in the gut may relate to this proposed mode of infection. First, young cells were found to be concentrated close to the anus. Second, cells in the posterior gut were often immobile, as were those found in the feces. Since the active organism appears to be an anaerobe, the immobile stage released in the feces may be an encapsulated or encysted form.

We have few clues to the nature of the relationship between the host and its symbiont. Fluorescence microscopy at wavelengths that cause red fluorescence of chlorophyll revealed red fluorescence at or immediately under the pellicular layer, but intact algal fragments were never observed within the organism itself; thus adsorption or absorption of macromolecules may occur, but ingestion of algal tissues probably does not. The location of protists close to the gut lining rather than throughout the food bolus suggests that they may not be involved to any large extent in primary digestion; this does not, however, preclude a digestive role with secondary or semidigested metabolites or a secretory role as a supplier of micronutrients to the host.

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