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The intestinal *Pronocephalidae* *(Vermes, Trematoda)* of the marine Iguana from the Galapagos Islands; a possible case of pure mutualism. [1, 2]

(Pronocephalidae (Vers Trématodes) dans l'intestin d'Iguanes marins des îles Galapagos : un cas possible de mutualisme)

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ABSTRACT

Comparison of autopsy findings on several marine iguanas in the Galápagos with those of a specimen transported to California that died with severe constipation after two years, leads the authors to suspect that the extremely numerous intestinal trematodes might, by mutual adaptation, have come to adopt a role in the digestive physiology of the hosts. There may thus be a mutualistic element in the relationship.

The Galápagos International Scientific Project (Jan.-March, 1964), under the auspices of the University of California Extension, Berkeley, took sixty scientists to the Archipelago made famous by Charles Darwin as a great natural laboratory for studying the processes of evolution.

Host :

One of the unique Galápagos species investigated was *Amblyrhynchus cristatus*, the marine iguana which lives on the lava-rock shore but swims and dives for its food, various types of seaweed. Past efforts to transplant *Amblyrhynchus* have been generally unsuccessful, as these reptiles almost invariably refuse to eat anything whatever in captivity. An elaborate attempt of the California Academy of Sciences to reproduce

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their natural environment, with lava rock and salt water tanks containing seaweed, likewise met with failure.

Because of these discouraging experiences, only two living specimens of *Amblyrhynchus* were brought back from the 1964 expedition. One of the authors (Lowenstein) found quickly that his iguana, a young male from Santa Cruz I., would not be tempted by any available meats or vegetables, including seaweed. Being a physician, he therefore proceeded to forcefeed the animal via a plastic tube introduced through the mouth and passed into the stomach. The exclusive diet was strained baby food (Gerber's mixed green vegetables) with an occasional addition of sea water, injected through the plastic tube with a 50 ml. glass syringe. The animal was fed two to three times a week and seemed to thrive.

Meanwhile the second specimen, an adult male from Hood I., had not eaten for three weeks and was moribund. At this point he was turned over to the junior author for care. He was fed in the same way as the smaller iguana, but given 100 ml. strained vegetables two to three times a week. Both animals were kept in the investigator's home in San Francisco, in a wooden box with an electric heating pad, and allowed to wander freely about the house, which they did, generally following the sun as it shifted its beams from one window to another.

At first the teeth and gums were traumatized by forcible introduction of the plastic tube and mouth infections supervened. These cleared up promptly with the addition of the antibiotic tetracycline to the food and did not recur, though tetracycline was stopped after one week. Occasionally an intestinal worm could be seen on the tube when it was withdrawn after a feeding.

The younger animal died suddenly after five months. It had apparently been well until its demise. No autopsy was done. The adult continued well and active for twenty months, when it had an episode of vomiting lasting one day, from which it seemed to recover completely. Two weeks later it expired during the night and was found dead in its box in the morning.

Autopsy Report (December 16, 1965).

1. Ascites (840 cc.), turbid and tinged with blood, in abdominal cavity.
2. Gross outer aspect of the digestive tract showed several regions of the intestinal coils critically distended and stuffed with blocks of hard material, alternating with spastic regions.
3. Esophagus intact, not scarred or stenotic.
4. Stomach with two hemorrhagic areas (15 mm. in diam.).
5. Small intestine partially eroded, very obvious epithelial exfoliation. Numerous small hemorrhagic patches.
6. Duodenal perforation, about 12 cm. from the pylorus.
7. Ileum, near ileocecal valve stenosed ; lumen reduced to 2 mm. in diam. over a length of 10 mm.

8. Colon showing alternate tight contraction of bowel wall muscles (lumen empty) and huge distentions filled with hard, dark brown-green putty-like material. By contrast the fecal matter of marine iguanas autopsied in the Galápagos Islands was much softer and more spongy.
9. Distal end of colon more or less haemorrhagic (patches, 3-6 mm. in diam.).
10. Sigmoid colon with very thin walls, distended near rupture point, due to hard, putty-like feces. Spastic rectum, with haemorrhagic patches.
11. Liver gray and paler than normal.
12. Gall bladder abnormally large and distended with bile.
13. Lungs showing congested areas, some acute and others more chronic, and also several alimentary fragments, indicative of inhaled vomitus.
14. Intestinal parasites (trematode worms) totally absent. Although thousands of these worms are normally found in the digestive tract of *Amblyrhynchus* autopsied in the Galápagos Islands, none was found in this specimen.

Discussion :

Duodenal perforation is reasonably the immediate cause of death. Dietary deficiency due to the artificial nutriment is, to all appearances, the prime cause in developing a fatal constipation, intestinal obstruction and vomiting.

However, even if the dietary deficiency takes a certain time to manifest itself and to kill the lizard, the fact that the animal lived over twenty months before dying is intriguing and leads to the following speculation.

Considering the powerful crawling habit of the worms, capable of maintaining the alimentary bolus soft and loose and opposing in that way their mechanical action to that of constipation, it is assumed that they retarded considerably the fatal ending. Unfortunately the trematodes existing in the intestine of the iguana at the date of its capture, died or were expelled slowly, one by one, as could be observed on several occasions by the second author, leaving the place of the deadly obstruction.

Trematodes :

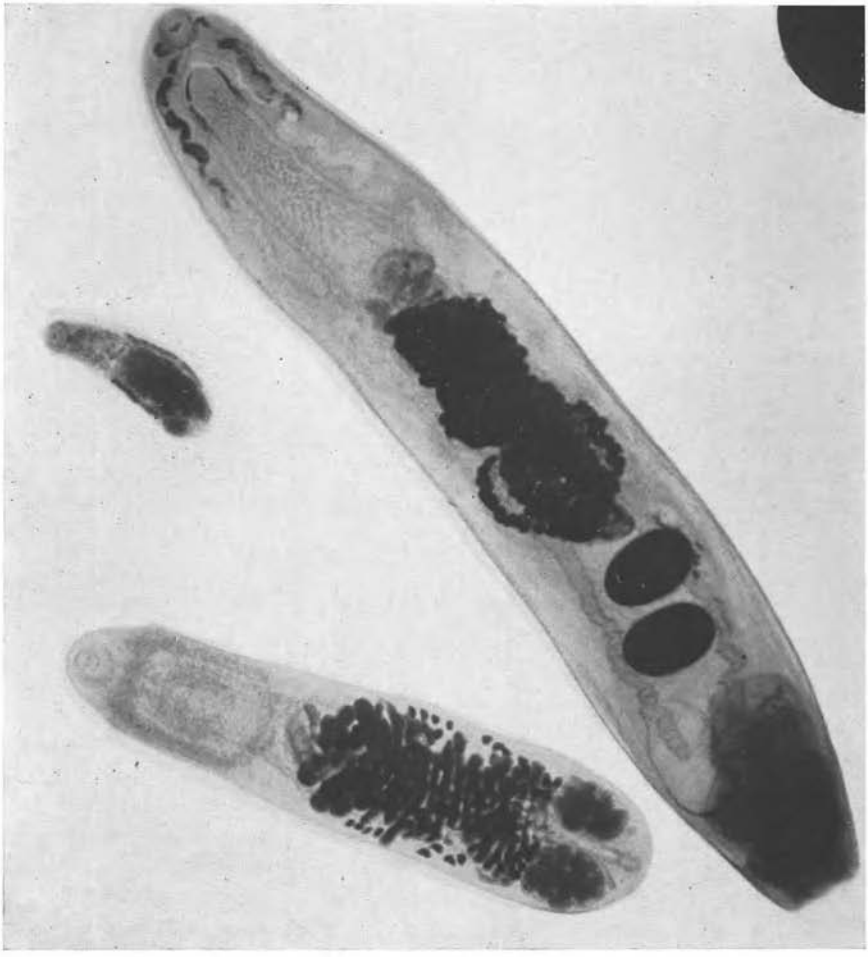
In 1938, Paul T. Gilbert described the three intestinal trematodes collected from marine iguanas by Dr. H. W. Manter, during the Allan Hancock Expedition to the Galápagos Islands, in 1934. These three species were recorded again by the senior author during the 1964 Expedition.

They are monostomes and belong to three different genera of Pronocephalidae : *Iguanacola navicularis, Myosaccus amblyrhynchi* and *Cetiosaccus galapagensis,* after Gilbert. In 1961, J. Baer and CH. Joyeux synonymized *Myosaccus* Gilbert with *Pyelosomum* Looss, 1899.

Very little is known of the biology of this important family. Skrjabin himself complained in writing in 1955 : « There is a great need for complementary studies on the biology of that group... ». By analogy with *Macravestibulum eversum,* the only

similar chelonian parasite of which the life cycle is known, it is probable that the iguana infests and reinfests itself by eating seaweeds bearing the metacercariae of pronocephalids fixed on their surface.

The senior author has observed the behavior of these worms *in situ*. All move freely, creeping on the intestinal walls as well as among the alimentary bolus.



Pronocephalids have no possibility of attachment. Their very small mouth is of no use in that respect and only serves for feeding (on chyme or on chyle). The larger species *Cetiosaccus galapagensis*, seems to be the principal agent of our present speculation, as it winds like a snake unceasingly among the alimentary bolus, in the company of many thousands of its fellows.

Pyelosomum amblyrhynchi (Gilbert, 1938) is the smallest (length 3-5 mm., width 1.1 to 2.2 mm.), most numerous in the stomach, but found all the way to the end of the colon, in the intestinal content as well as creeping among the intestinal villi, apparently using both chyle and chyme for its food. Several hundred occur in a single host.

Iguanacola navicularis (Gilbert, 1938) is approximately twice as long (length 4-10 mm. width 1.1-2.2 mm.), most numerous in the stomach but found all the way to the end of the colon — in the intestinal content as well as crawling among the intestinal villi — apparently using both chyle and chyme. Hundreds in a single host.

Cetiosaccus galapagensis (Gilbert, 1938) still, longer than the former, but proportionally thinner (length 6.5 to 26 mm., width 0.8 to 2.4 mm.). They wind through the intestinal content, actively and evidently loosening the seaweed bolus from the stomach to the rectum. They obviously prefer the chyme. More than two thousand per host (may be 5.000 in large iguanas).

Mutualism :

Parasitism does not imply that an animal guest must feed on the living tissues of its victim. On the contrary, most parasites lead a symbiotic existence with their hosts. Though they are not frequent, there are also cases of mutualism in which the guest is beneficial to the host : *Escherichia coli* in man ; cellulophagous or xylophagous flagellates and ciliates in the stomach of ruminants and in the digestive tract of termites and roaches and other arthropods ; azotobacteria in plants.

That pronocephalids may be necessary to marine iguanas is suggested by the following considerations. It appears from the autopsy that constipation was at least a contributing cause of death. Although production of feces was irregular during life, during the last day there was very little, and there was hard impacted material in the ileum and colon. It is possible that the low-residue diet of strained vegetables — as compared with the bulkier algae of the Galápagos — may ultimately have had a deleterious effect. But it is more probable that the thousands of intestinal worms (of relatively large sizes) normally found in marine iguanas, have an important role either in aiding digestion, or in maintaining gastro-intestinal motility, and their gradual expulsion may have led to constipation and death.

The following experiment, to be carried out at the Darwin Station of Santa Cruz (Galápagos Islands), would be conclusive :

1. Isolate iguanas and feed them according to the method of the junior author ;
2. Continue until almost all the pronocephalids are expelled and the constipation becomes apparent (decrease of droppings, hard impacted material palpable in the intestine) ;
3. Then add to the diet a massive quantity of pronocephalid metacercariae (collected on seaweeds).

If constipation relaxes and if the feces become normal again, proof of mutualism would be obtained. This experiment would necessitate the autopsy of a small number of specimens at the crucial points of the experiment.

Conclusion

Considering, 1) the numerical importance of the trematodal infestation in all the marine iguanas, 2) the apparent harmlessness of that mass of relatively large trematodes, 3) their comportment apparently beneficial to the host, 4) the visible adaptation of the trematode-guests in massive number on the unharmed iguana-hosts, for a long time, possibly millions of years, 5) the nature of the accidents occurring in the absence of trematodes, and 6) the acknowledgements by different scientists and naturalists of their failures in attempting acclimatization of *Amblyrhynchus cristatus* out of the Galápagos circle, we assume that those worms could be of capital importance in the maintenance of their hosts in good health.

Summary

Observations are reported on the Galápagos marine iguana (*Amblyrhynchus cristatus*) maintained alive in a private home in San Francisco for twenty months by force-feeding with baby food (mixed green vegetables). On autopsy the apparent cause of death was intestinal perforation, probably due to constipation and intestinal obstruction. The most striking finding was the complete absence of the intestinal trematodes which abound by the thousands in the animals in their natural habitat, the Galápagos Islands. It is speculated that this could be a case of mutualism, in which the host is as dependent for survival on the worms as the worms on the host.

Résumé

Deux iguanes marins (*Amblyrhynchus cristatus*) ramenés des îles Galápagos aux cours de l'expédition de 1964, furent maintenus en vie dans la maison du second auteur. L'un d'eux survécut pendant un peu plus de vingt mois, grâce à une alimentation forcée (tubage intra-stomacal) composée en majeure partie d'aliments du premier âge (mélange de légumes verts). A l'autopsie on décela une perforation duodénale, cause directe et finale de la mort. La cause primaire étant, selon toute apparence, une sévère constipation avec obstruction intestinale, accompagnée de vomissements. La découverte d'autopsie la plus frappante fut l'absence totale de vers intestinaux (Pronocephalidés), toujours présents par milliers chez les iguanes marins. Les plus grands de ces vers (*Cetiosaccus galapagensis*) rampant activement dans les masses du bol alimentaire, les ameublissent visiblement en les maintenant légères et spongieuses, favorisant ainsi leur circulation. Ces associations de causes à effets ont amené les auteurs à penser qu'il s'agissait d'un cas de mutualisme, où l'hôte et son ver parasite se doivent mutuellement la vie.

Sumario

Observaciones son reportadas en la iguana marina de Galápagos (*Amblyrhynchus cristatus*) sustenida en hogar privado en San Francisco por 20 meses, alimentandole forciblemente con comida de niños (vegetales verdes mezcladas). En autopsia la causa apa-

rente de muerte fue perforación intestinal. El descubrimiento mas notable fue la absencia completa de trematodas intestinales que abundan en miles en este animal en su habitación natural, las Islas Galápagos. Es especulado que esto podría ser un caso de mutualismo, en cual el huesped es tan dependiente para supervivencia en los guzanos como son dependientes los guzanos en el huesped.

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