EFFECTS OF MICROGRAVITY AND HYPERGRAVITY ON INVERTEBRATE DEVELOPMENT

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SUMMARY

Invertebrates, and especially insects, have often been used in research on the biological effects of microgravity and hypergravity, both in the United States and in the Soviet Union.

The data suggest that abnormal gravity loads do not increase the rate of mutations in these lower animals. Moreover, insects such as *Drosophila melanogaster* and *Tribolium confusum* have been able to reproduce aboard unmanned and manned space satellites, though no precise quantitative data have been obtained on mating competence and various aspects of development.

Our own research with *Drosophila* flown on Soviet Cosmos spacecraft suggests that flight behavior is seriously disturbed in insects exposed to microgravity, which is reflected in increased oxygen utilization and concomitant life shortening. The decrease in longevity was less striking when the flies eclosed in space, which suggests that they could adapt to the altered gravitational environment when maturation of flight behavior took place in microgravity.

The reviewed data suggest that further research on the development of invertebrates in space is in order for clarification of the metabolic and behavioral effects of microgravity and of the development and function of the orientation and gravity-sensing mechanisms of lower animals.

INTRODUCTION

Like all other animals, invertebrates have evolved under the influence of the Earth's gravitational field. Therefore, it is reasonable to assume that gravity (g) has played a key role in shaping their structure and function, and that exposure to hypergravity or microgravity must result in a variety of cellular and physiological reactions. This has been recognized over the years by NASA advisory committees, which have specifically recommended the implementation of space-biological research on invertebrates. The 1970 Summer Study of the National Academy of Sciences pointed out that the exposure of invertebrates to near weightlessness may be useful for the study of the statolith mechanisms which play a role in orientation (ref. 1). In a more recent report, the Space Sciences Board of the National Academy of Sciences (ref. 2) notes that, "In the fields of cell, plant and invertebrate biology, the biological questions that may be best examined with space techniques relate to the responses of organisms to gravity by their growth, form and orientation." Further, according to the report, "As with plants, the influences of gravitational acceleration on invertebrates may be considered under the two broad categories of effects mediated by (i) specialized receptors such as proprioceptors, acceleration receptors, and organs containing statoliths and (ii) small shifts in the distribution of organelles or similarly non-specific mechanisms."

To my knowledge, the first studies on invertebrates exposed to hypergravity were performed by Wunder and Luther (ref. 3), who showed that when Drosophila larvae were centrifuged at 5000 g, their rate of growth and final size attained were lower than those found in noncentrifuged controls.

Because of their small size and simple housing and feeding requirements, many invertebrates are ideal experimental animals for spaceflight research. This has been recognized by the Soviet space biologists who have often used the most thoroughly investigated invertebrate, i.e., Drosophila melanogaster, in their systematic program of research on board unmanned and manned satellites (refs. 4 and 5). As far back as 1960, fruit flies were exposed to the space environment for 24 hr in an unmanned Soviet "Spaceship-Satellite" and, in 1961, larval cultures and imagoes of D. melanogaster accompanied the first cosmonaut Yuri Gagarin in his orbital flight on board "Vostok" 1. Since that historical mission, fruit flies have logged the impressive total of about 2500 hr of exposure to near weightlessness on U.S.S.R. unmanned satellites and 4000 hr on manned spacecraft (tables 1 and 2). By contrast, the corresponding figures of exposure of D. melanogaster to the space environment on American satellites are only 48 hr for unmanned biosatellite flight and 0 hr for experiments performed on manned vehicles, although a variety of other invertebrate species did receive some attention (table 3). Unfortunately the majority of U.S. spaceflight studies on invertebrates used them as biological radiation dosimeters, rather than as experimental subjects for developmental or other non-radiobiological studies.

The availability of the Shuttle Spacelab will allow the realization of further invertebrate research in space. This research should be encouraged not only because it is technically uncomplicated, but also because it will provide important scientific data. It is true that numerous observations, including NASA's collaborative research with the Soviet geneticist G. P. Parfenov (refs. 6-9), suggest that exposure to weightlessness does not influence the fundamental processes involved in growth and morphogenesis. Moreover, since weightlessness per se does not have a mutagenic effect, it may seem pointless to perform further flight experiments on invertebrates. However, it should be stressed that most space-biological research (except for the thorough studies of Parfenov on Drosophila genetics, ref. 10) has been poorly controlled; therefore, the possibility exists that the more rigorous experiments feasible in space laboratories may detect quantitative changes in developmental parameters which have thus far escaped detection. Moreover, we should keep in mind that many invertebrates, and particularly the highly evolved insects (figs. 1 and 2), have gravity-sensing mechanisms which rival in their sensitivity and sophistication those of mammals. It has been pointed out that insects may have been the first animals which left the sea environment (where the gravitational pull of the Earth is counteracted by buoyancy) to successfully adapt to life on solid ground and even to master controlled flight (ref. 3). This expansion of the ecological niche of invertebrates was accompanied by the development of the extremities needed to support motion both on the ground and in air (figs. 3-7), and position and acceleration sensing devices such as the bristle fields found at the insect body joints and the flight-supporting halteres (figs. 7-9). Obviously, the sensory deprivation associated with the lack of gravity in space must result in a host of behavioral reactions which so far have not been satisfactorily observed or quantified. Furthermore the development of these gravity-sensing systems may be altered in microgravity or may not even be initiated.

If an excessive caution may prevent the realization of interesting flight experiments on invertebrates, the naive attitude that, since gravity is an important component of the environment, microgravity may induce a garden variety of changes at practically every level of biological organization must also be avoided. As often stressed by the Space Sciences Advisory Boards (refs. 1 and 2), spaceflight experiments are very expensive and "fishing trips" in search of ill-defined responses to weightlessness are not justifiable. It is the feeling of the NASA Advisory Committee that, after nearly a quarter century of biological spaceflight both by humans and lower animals, the era of the exploratory flight experiments should come to an end and a second generation of studies (to be performed by scientist-astronauts aboard the Shuttle Spacelab) should deal with testable hypotheses on gravity-dependent processes, which are strongly supported by the data from previous spaceflights and the results obtained in ground-based laboratories.

For biologists interested in flight experiments, the remainder of this paper will focus on the main data on invertebrates, many of which were published in Russian reports not easily accessible to Western scientists. A brief discussion of the scientific relevance of these data and some ideas about working hypotheses worth testing in future flight experiments are presented.

EXPERIMENTAL DATA

Spaceflight Research on *Drosophila*

It is not surprising that, since *Drosophila* enjoys a well-deserved popularity as an excellent model for genetic studies, research on the mutational effects of altered-gravity loads has focused on this insect.

Early spaceflight research by both Soviet (ref. 4) and American geneticists (refs. 13-16) suggested that microgravity or cosmic radiation, or an interaction of both, caused an increase in mutations. However, a more critical analysis of the data as well as the results of many other flight experiments from the Soviet Union (tables 1 and 2) showed unequivocally that microgravity is not mutagenic. Similarly, though there have been reports of morphological abnormalities in fruit flies which had developed in space, it could not be established that these abnormalities were the result of microgravity instead of vibration, abnormal temperature, faulty nutrition, or other poorly controlled factors present during spaceflight (ref. 4). Our own observations on fruit flies which were conceived, developed, and eclosed in space aboard the Cosmos 936 biosatellite support the view that microgravity does not exert a detrimental effect on the processes of cell growth, division, and differentiation which are involved in normal morphogenesis (figs. 2-7).

The first experiments ever performed on animal reproduction in space took place in 1962 aboard the manned satellites Vostok 3 and 4, with the assistance of cosmonauts A. G. Nikolaiev, P. R. Popovich, and V. F. Bykovsky. In their report of that pioneering experiment, Antipov *et al*. (ref. 17) comment that, "While planning these experiments one could expect that weightlessness would affect processes of copulation and laying of eggs." The fruit flies proved to be more adaptable than expected since they were able to mate and lay eggs in the microgravity environment. This interesting result does not rule out the working hypothesis that microgravity may exert a negative influence on reproduction. As pointed out by Antipov *et al*., these experiments have shown that fecundation, laying of eggs, and development of *Drosophila* under conditions of microgravity with a duration of up to 4 days can proceed normally. However, the data obtained were only of a qualitative nature and do not allow us to determine quantitatively changes in mating behavior or in the viability of embryos, larvae, etc.

In contrast to the early stages of the Drosphila life cycle, which are not grossly altered by microgravity, the last stage, namely the aging process, probably is altered by abnormal gravity loads (refs. 6-9). This effect is suggested by our preliminary finding that fruit flies which were exposed as young adults to microgravity for nearly 20 days showed a strikingly reduced life span when allowed to age normally upon return to our NASA laboratory (fig. 10). Our working hypothesis is that flies which are exposed to microgravity after completing maturation on the ground cannot control their flying behavior in the absence of the usual gravitational cues. This inability, in turn, results in a disordered motor activity, with concomitant increase in oxygen utilization and (in agreement with the predictions of the rate-of-living and free radical theories of aging (refs. 6-9). We further assume that imagoes eclosed in space adapt or learn to control flight in microgravity during the first hours of adult life, when the insects may be more receptive to the function-molding inputs of the environment. This adaptation must result in a less wasteful utilization of oxygen and, therefore, in a life span at microgravity similar to that found under normal 1-g conditions.

As will be noted below, our interpretation of the Cosmos data is supported by the finding that exposure of fruit flies to continuous rotation in horizontal clinostats results in both an increased level of activity and a significant shortening of life span.

Effects of Hypergravity and Clinostat Rotation on Drosophila

A complete understanding of the role of gravity in invertebrate biology cannot be obtained without exposure of these animals to high gravitational fields. Again, the most comprehensive studies on the effects of high-gravity loads on growth and development have been carried out on D. melanogaster because Drosophila larvae are ideally suited for refined quantitative determination of the efficiency of growth, since they show an almost perfect linear correlation between the logarithm of their volume and the passage of time (ref. 18). Wunder et al. (ref. 18) took advantage of this for demonstration that, though growth was possible in fields as intense as 5000 × g, both the rate of growth and the final size attained were below the values seen in larvae maintained at 1 × g. The growth rate decreases as the field intensity increases beyond 1000 × g. Paradoxically, at fields of 500 × g there is a 25% increase in growth rate. As in previous experiments on wheat seedlings (ref. 19), the larvae showed a faster than normal growth upon removal from the centrifuge. This interesting phenomenon was accompanied by a decreased oxygen utilization, which suggests that, following exposure to high-gravity loads, the bioenergetic processes supporting growth became more efficient (ref. 20). This metabolic effect of exposure to hypergravity appears to be a universal phenomenon, since an increased rate of growth has been observed in turtles exposed to 5 × g and mice kept at 1.5 × g. On the other hand, mice centrifuged at 4 × g grew at a slower rate than "pair fed" controls (ref. 3). This last finding results from the fact that an animal must dissipate energy in direct proportion to its weight to maintain body position and locomotion against the pull of gravity. Small increases in body weight resulting from exposure to moderately raised gravity fields in the centrifuge may be counteracted without an effect on growth by increasing food intake and metabolic efficiency. However, there is a limit to the amount of food that an animal can ingest; therefore, centrifugation at high gravity levels must result in the diversion of a considerable amount of energy to be wasted counteracting the pull of gravity, and a concomitant reduction in the amount of nutrients available for cell growth and replication (ref. 20).

Preliminary research on the effects of *Drosophila* rotation in clinostats has yielded interesting results. It should be noted that clinostats do not provide an exact replica of the microgravity environment of space. Nevertheless, we are of the opinion that rotation about the horizontal axis using clinostats, with continuous change in the direction of the gravity vector, may result in disorientation phenomena akin to those occurring in microgravity. This view is supported by the finding that, though the development of *Drosophila* was uninfluenced by clinostat rotation, flies showed an increased locomotion and decreased life span when kept in the clinostat from eclosion to death (ref. 21).

Tribolium Experiments

After *Drosophila*, the flour beetle *Tribolium confusum* is the most often used invertebrate in the biological flight experiments of both the United States and the Soviet Union. A pioneering experiment by Buckhold *et al*. (ref. 13) dealt with the effects of microgravity and the combined effects of microgravity and gamma radiation on mutations and wing development in beetles exposed to the space environment aboard the U.S. spacecraft *Biosatellite II*. The beetles were in the pupal stage at the start of their 2-day exposure to spaceflight. The results suggested that microgravity did not affect survival of the insects. On the other hand, pupal period,wing abnormalities, and mutations were significantly increased. The conclusion was that some factor in spaceflight, probably microgravity, was responsible for the effects observed, though a temperature drop occurring before retrieval of the flight capsule could have played a role.

More recently, flour-beetle eggs have been used in the radiobiological experiments performed aboard Apollo 17 and during the Apollo-Soyuz mission (ref. 16). apparently the eggs were extremely sensitive to the high-energy particles of the cosmic flux. Hatching frequency was significantly reduced, and after hatching there was a high mortality at the larval stage. Developmental abnormalities (e.g., a curved abdomen, fusion of body segments, and splitting or shortening of elytra) showed a striking increase from 2.5% in the controls to 48% in the space beetles.

Another investigation on flour-beetle development in space has been performed by G. P. Parfenov on *T. castaneum* exposed to weightlessness aboard the unmanned biosatellite *Cosmos 605* (ref. 10). There was not enough time for the complete cycle of development of the beetles to be completed during the flight, which lasted about 20 days. The specimens placed aboard were at the embryo, larva, and pupa stages. The data showed no detrimental effect of weightlessness on the processes of hatching of larvae, pupation, or eclosion. Moreover, the survival rate of the specimens at all stages of development was about the same as for controls.

Further research on the effects of microgravity on the biology of *Tribolium* was performed on the beetles flown in the manned space station *Salyut 6*. In this long-duration experiment, *T. castaneum* completed its developmental cycle, from fertilization to the eclosion of the mature imagoes of the next generation, in a normal way. There were no significant genetic changes (ref. 22). This lack of response to altered gravity is in agreement with a clinostat study showing that rotation on this instrument did not result in genetic changes or abnormal development in T. confusum and T. castaneum, even though the insects were exposed to an abnormal gravity vector during eight consecutive generations (ref. 23).

Flying Behavior in Microgravity

In 1982 the Shuttle STS-3 carried an insect flight experiment designed by Todd E. Nelson, an 18-yr old high school senior from the Southland 500 Schools in Adams, Minnesota (Philpott, D. E. and Miquel, J., unpublished observations). The experiment exposed three species of insects to microgravity to explore the disturbances in flight behavior. Apparently the lack of gravity did not significantly interfere with the flight of Velvet Bean Caterpillar moths (Anticarsia gemmatalis). On the other hand, as viewed on videotape, worker bees (Apis mellifera) were unable to sustain a controlled flight. They appeared to float in the container throughout the Shuttle mission and occasionally tumbled when they used their wings, rather than exhibited normal directional flight. The center of gravity of bees is located dorsally behind the wings, which may be responsible for the observed pitching, since the lack of a counterweight at microgravity probably results in a loss of balance. House flies (Musca domestica) seemed more successful than bees in establishing normal flight patterns in microgravity.

Insects differ in the degree of sophistication of their flight mechanisms. Thus, bees have two pairs of wings and lack halteres (figs. 5 and 6), while house flies and other diptera have only one pair of wings (fig. 7), with the other pair transformed into gyrostat-like halteres (figs. 7-9). This refinement of the flight apparatus may give the flies a much more accurate perception of the body accelerations sustained during flight (and a better postural control) than is available to bees and other four-winged insects. In the case of moths, the large ratio of wing area to body weight may play a role in the preservation of flying ability in weightlessness.

Besides the striking differences in flying behavior between house flies and bees, exposure to microgravity also resulted in another interesting effect on locomotion. During spaceflight bees were not able to crawl on the walls of their housing unit as were flies. This difference in walking ability between flies and bees during exposure to weightlessness may be related to the different functional design of their feet. Thus, while flies have an adhesive structure (fig. 3), which allows clinging to smooth surfaces, bees have claws surrounding a footpad (fig. 4).

Our electron microscopic study of the Shuttle-flown bees revealed a perfectly normal structure of the exoskeleton, suggesting that despite their difficulty in controlling flight, the bees had not been injured by bumping against the walls of the housing unit.

Although this experiment was not directly concerned with the subject of this review, i.e., development in space, it has clear developmental implications.

In our opinion it is advisable to investigate further the flying behavior of insects which are exposed to microgravity in space after developing on Earth, and of insects which have eclosed in a space laboratory. The hypothesis to be tested is that insects which develop and mature in space may control flight in microgravity better than those exposed to microgravity after completing their development at $1 \times g$.

Flight Experiments on Other Invertebrates

Ascaris eggs and Artemia salina cysts have been used in several Soviet spaceflights for investigation of radiation effects (ref. 5). Cysts of the crustacean Artemia salina and adult parasitic wasps (Habrobracon juglandis) were also exposed to microgravity in the U.S. Biosatellite II (ref. 16). In these early experiments no conclusive effects on the developmental process could be shown. In better controlled studies, Artemia salina eggs exposed to the space environment during the Apollo-Soyuz mission, Ruether et al. (ref. 16) showed a delay in hatching and an increase in developmental anomalies, especially in the extremities and the abdomen. Further research on the larvae of nematodes (Nematospiroides dubius) and grasshopper eggs (Carausius morosus) flown aboard Apollo 16 and during the Apollo-Soyuz mission, respectively, failed to show a significant effect on development (ref. 16).

An earlier experiment on sea urchin eggs (Arbacia punctulata) was flown in the Gemini 3 mission, but no data were obtained because of a technical failure of the housing unit (ref. 16).

Only one flight experiment on Arachnida has been performed to date, that of the high school student Judith Miles, showing that cross spiders (Araneous diadematus) spin finer threads at microgravity (in Skylab 3) than on the ground (ref. 16). As in the case for the flying behavior of insects, the net-webbing of spiders may be a behavior worth studying on animals developed in space.

CONCLUSIONS

The reviewed data support the concept that the cellular processes involved in genetic change, mitosis, and differentiation are insensitive both to microgravity and hypergravity, as well as to rotation in horizontal clinostats. Thus the experimental gravitational research on invertebrates supports the early views of Morrison (ref. 24), according to which, "DNA processes will not be affected by zero gravity." The probable reason is that biochemical reactions are controlled by electromagnetic forces which are much more intense than gravitational fields (ref. 25).

At a higher level of organization (i.e., that of the subcellular organelles), invertebrate response seems to differ from that of plants exposed to abnormal gravity loads. In plants exposed to microgravity aboard Soviet satellites, the starch granules (statoliths) were distributed uniformly throughout the cytoplasm, whereas in ground-based controls the starch accumulated at the bottom of the cells (ref. 25). No such changes in distribution of subcellular particles or organelles have been seen in invertebrate cells exposed to microgravity or hypergravity; however, no one has looked at the statolith-like structures located in the halteres of insects fixed before reentry to a normal gravitational environment. Perhaps the high viscosity of the cytoplasm of animal cells and their cytoskeletons prevent a redistribution of their structures when exposed to microgravity.

At the physiological and behavioral levels, it seems well documented by numerous flight experiments that insect reproduction can take place in microgravity. However, there is a lack of precise quantitative data on such important parameters as duration of development from fertilization to eclosion, and number and success of copulations in comparison to the values obtained in ground-based laboratories. As we just discussed, previous research from the U.S. and the Soviet Union has emphasized radiation biology and genetics with an almost total neglect of the physiology and behavior of invertebrates exposed to microgravity. This, in my opinion, justifies the experimental testing of hypotheses, such as the following:

1. Development may be slowed down in microgravity because of disturbed larval behavior with decreased food intake.

2. There is a decrease in male mating competence and female fertility in space.

3. Insects endowed with halteres can better control flying behavior in microgravity than can other insects.

4. Insects eclosed in space will be more adept at controlling flight and performing mating than those tested in space after eclosing on the ground because of adaptation to microgravity during the first hours of their imaginal life.

5. Drosophila strains showing geotactic responses may lose these responses following development and eclosion in space.

6. Invertebrates which have developed in microgravity may show altered behavior (locomotion, flight, taxis, and mating) when tested afterward in Earth-based laboratories.

7. Development of invertebrate gravity-sensing systems will not occur normally in microgravity.

The preliminary observations on irregular flight and net-webbing in insects and spiders exposed to microgravity suggest that further behavioral research in a broad selection of invertebrates may prove very rewarding in future flight experiments. As pointed out earlier, a comparative study of the effects of development on flying behavior of insects endowed with different flying mechanisms seems worth doing. This area of research is in agreement with the recommendations of the National Academy of Sciences Advisory Board (ref. 1), according to which, "Long-term exposures to low-g conditions probably will induce behavioral changes which are qualitatively different from those resulting from short term exposures during which significant adaptations do not occur. Such changes will prove to have both theoretical and practical interest." The Advisory Board further notes that, "One of the fundamental questions involved in future spaceflights is whether animals born and reared in a gravity-free environment exhibit normal anatomic, physiological and behavioral patterns upon return to earth."

In addition to the research on flight mechanisms and geotaxis (fig. 11), it is advisable to perform well-controlled experiments aboard the Spacelab on the quantitative aspects of mating. Among all components of reproduction, only mating may show a clear gravity-dependence, because it requires a high degree of neuromuscular coordination and postural control. Thus, a comparative study of the mating performance of insects showing complex courtship behaviors may provide valuable information both for understanding of invertebrate reproduction and of gravity-sensing mechanisms. Small insects could be conveniently housed aboard Spacelab in an escape-proof unit designed in our NASA laboratory (fig. 12).

In view of the genetic bias of most space biologists, it is not surprising that Drosophila has been the most widely used invertebrate in spaceflight research.

There is an obvious need for broadening the studies of development in space to other insect species and to lower invertebrates. It is doubtful that their embryonic development will be influenced by microgravity, in view of the negative results obtained on *Drosophila* and *Tribolium*. Nevertheless, gravitational research on such diverse postural perception mechanisms as the lyriform organ of the spider (ref. 26) and the antennal-socket setae of the microcrustacean water flea (ref. 27) may contribute to the understanding of the orientation mechanisms of lower animals.

The ultimate goal of research in gravitational biology is to provide a unifying view of the role of gravity in shaping structure and function. The present literature survey suggests that, largely because of the extant invertebrate research, the concept that abnormal gravity loads may influence cell genetics has fallen into disrepute (ref. 28). On the other hand, the invertebrate data lend support to the interesting hypothesis that, though altered gravity is not mutagenic, both hypergravity and microgravity trigger interesting somatic responses because of their effects on metabolic rate (refs. 29-34). In addition, microgravity has a disorienting effect that influences energy metabolism indirectly because of its effects on locomotion and muscle workload (figs. 13).

Because of the richness and predictability of invertebrate behavior and the case with which these animals can be incorporated into flight experiments, we believe that future research on these animals in space will contribute much to our understanding of the influence of gravity and the absence thereof on invertebrate behavior and development.

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TABLE I.- *DROSOPHILA* FLIGHT EXPERIMENTS FROM THE SOVIET UNION (ref. 5).

Year	Mission	Flight duration (days)
1960	Spaceship-Satellite 2	1
1961	Spaceship-Satellite 4	0.06
1968	Zond 5	7
1968	Zond 6	7
1970	Zond 8	7
1973	Cosmos 605	21
1974	Cosmos 690	21
1975	Cosmos 782	19.4
1977	Cosmos 936	21
1961	Vostok 1	0.08
1961	Vostok 2	1
1962	Vostok 3	4
1962	Vostok 4	3
1963	Vostok 5	5
1963	Vostok 6	3
1964	Voskhod 1	1
1965	Voskhod 2	1
1971	Soyuz 10	2
1973	Soyuz 17	29.5
1975	Soyuz 18	63
1976	Soyuz 21	49
1978	Soyuz 27	5

The Spaceship-Satellites Zond and Cosmos were unmanned biosatellites. In the Vostok, Voskhod, and Soyuz the cosmonauts assisted in the implementation of the experiments during spaceflight.

TABLE II.- OTHER SOVIET FLIGHT EXPERIMENTS ON INVERTEBRATES (ref. 5).

Year	Mission	Organism
1962	Vostok 3	*Ascaris* (eggs)
1962	Vostok	
1970	Zond 8	*Tribolium castaneum*
1973	Cosmos 605	
1975	Soyuz 18	
1975	Cosmos 782	*Artemia salina* (cysts)
1977	Cosmos 936	

TABLE III.- ORGANISMS USED IN U.S. BIOLOGICAL EXPERIMENTS IN SPACE.

Year	Mission	Flight duration (days)	Organism
1967	Biosatellite 2	2	Artemia salina (cysts)
1967	Biosatellite 2	2	Tribolium confusum (pupae)
1967	Biosatellite 2	2	Drosophila melanogaster (larvae)
1967	Biosatellite 2	2	D. melanogaster (pupae and adults)
1967	Biosatellite 2	2	Habrobracon juglandis
1972	Apollo 16	11.1	A. salina (eggs)
1972	Apollo 16	11.1	Nematosporoides dubius (larvae)
1972	Apollo 17	12.6	A. salina (eggs)
1972	Apollo 17	12.6	Carausius morosus (eggs)
1972	Apollo 17	12.6	T. confusum (eggs)
1973	Skylab 3	59	Araneous diadematus (adult)
1975	Apollo-Soyuz	9	A. salina (eggs)
1975	Apollo-Soyuz	9	T. confusum (eggs)
1975	Apollo-Soyuz	9	C. morosus (eggs)
1975	Cosmos 782	19.5	D. melanogaster (larvae, pupae, adult)
1976	Cosmos 936	18.5	D. melanogaster (eggs, larvae, pupae, adults)
1982	Shuttle STS 3	5	Apis mellifera (adults)
1982	Shuttle STS 3	5	Anticarsis gemmatalis
1982	Shuttle STS 3	5	Musca domestica

(Modified from ref. 29)

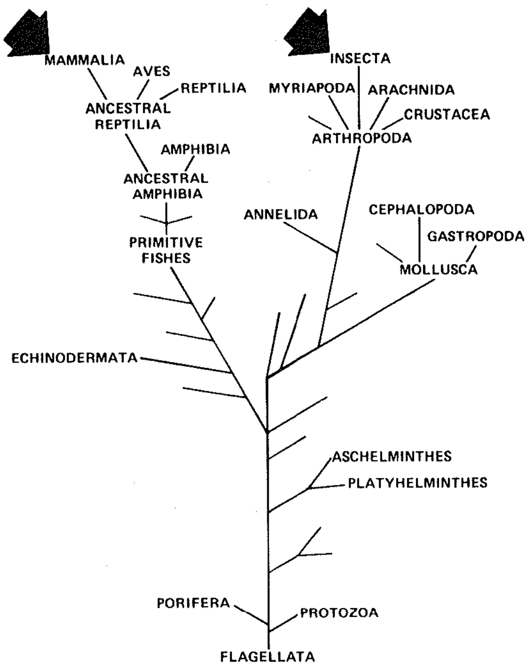


Figure 1.- This evolutionary tree shows the two diverging branches of animals leading to mammals (among the vertebrates) and insects, which are the most abundant and evolved invertebrates. Insects have been often used in the spaceflight programs of both the United States and the Soviet Union; it can be expected that, because of the richness and predictability of their stereotyped behavior, they will remain favorite experimental animals in future spaceflight research (from refs. 11 and 12).

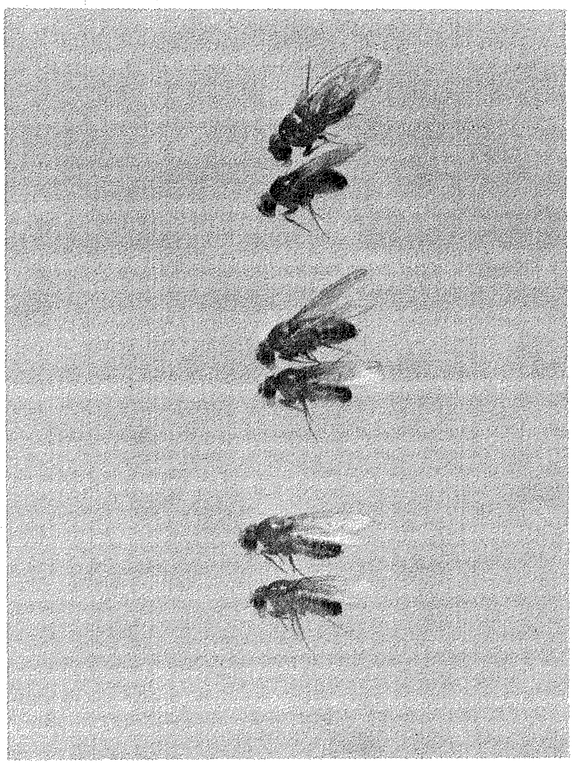
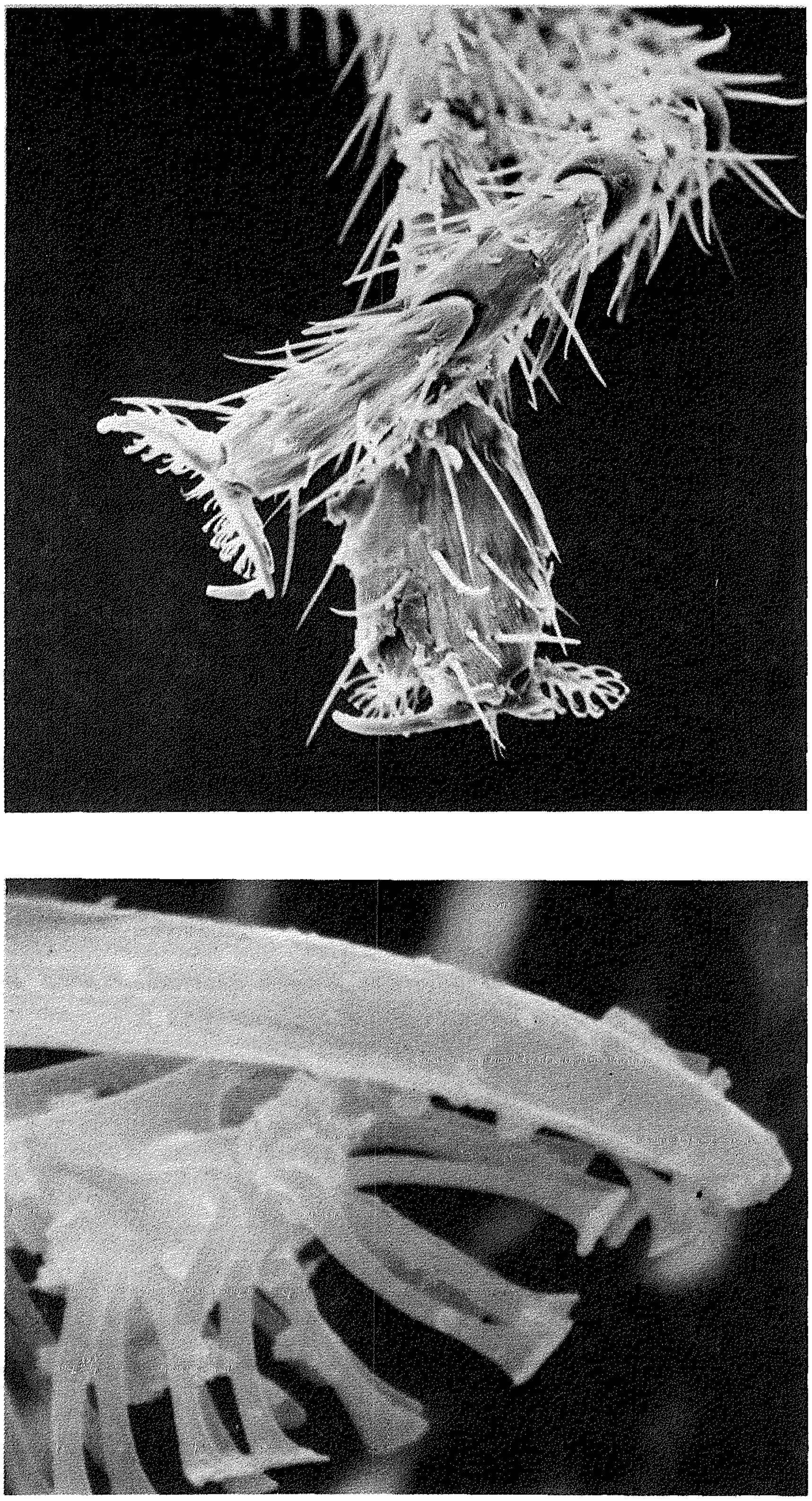


Figure 2.- Drosophila melanogaster has been used for extensive studies on the effects of microgravity on mutations. Moreover, in two collaborative U.S.-Soviet experiments flown in Cosmos biosatellites, other biological parameters such as development and aging were also investigated. In this illustration, we show male and female flies which developed on the ground (upper couple), at 0 × g (middle couple), and in the satellite in a centrifuge at near 1 × g (bottom). It is apparent that microgravity did not result in abnormal morphogenesis (ref. 7) (magnified 12 times).

Figure 3.- Scanning electron micrographs of legs and feet of D. melanogaster, showing nails and adhesive structures (ref. 8) (magnified 500 and 7000 times).



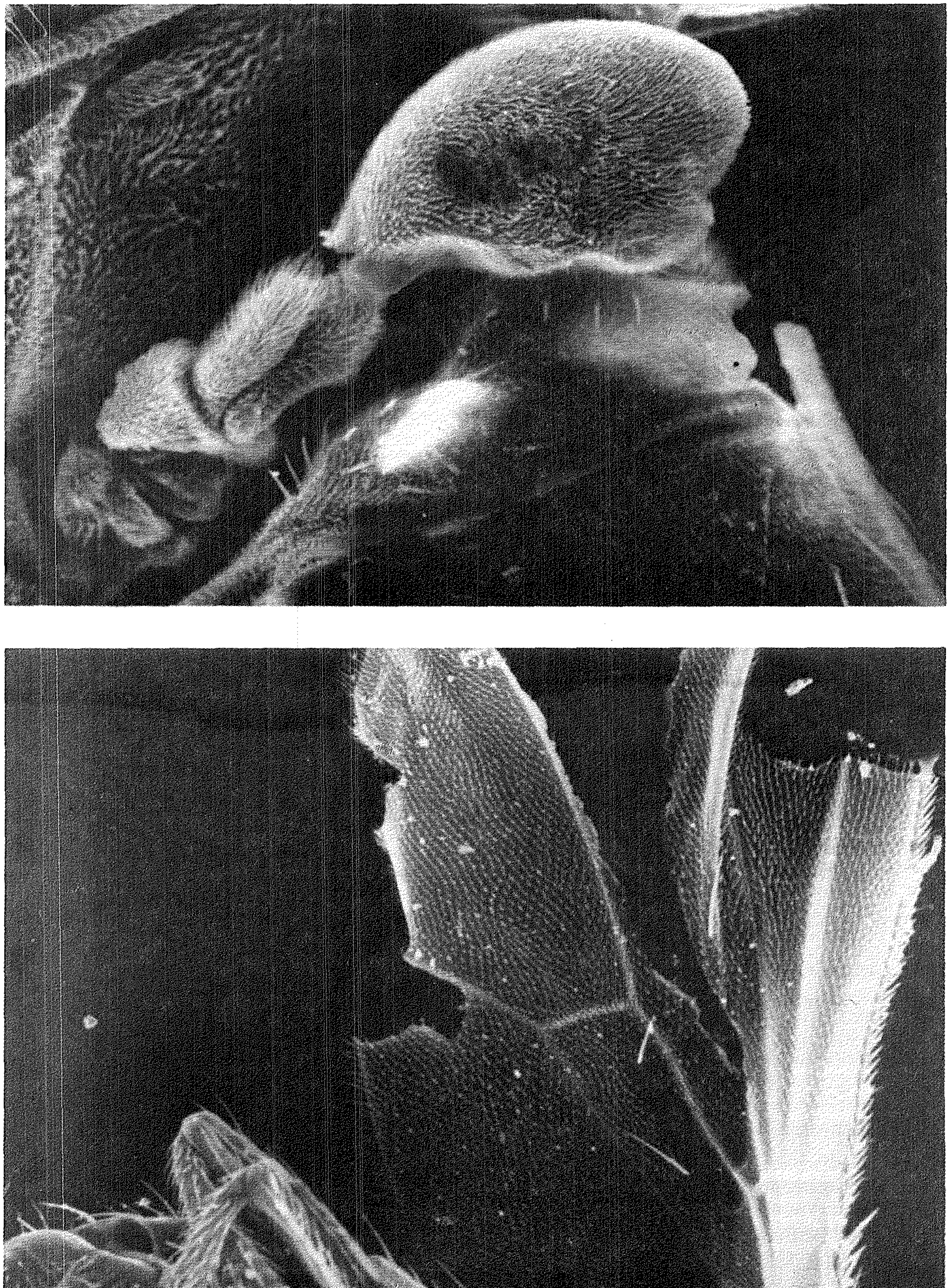


Figure 4.- Gyroscope-like haltere of *Drosophila* which allows a very precise control of pitch and roll during flight. Broken wing in a fly exposed to microgravity in space (ref. 8) (magnified 300 times).

Figure 5.- Foot of a worker honey bee which was flown aboard the Shuttle (ref. 24) (magnified 3000 times).

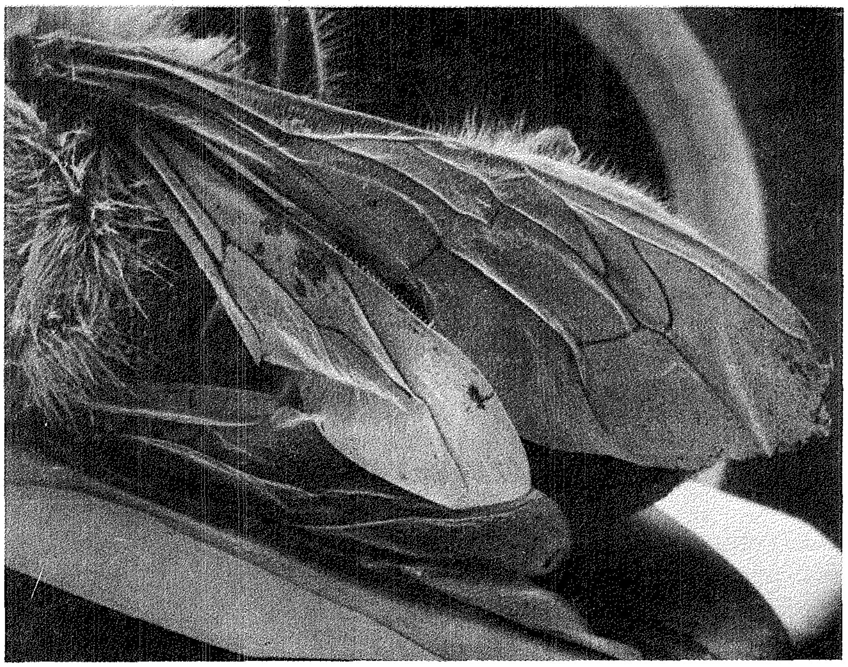


Figure 6.- Double wing of space-flown bee (ref. 24) (magnified 20 times).

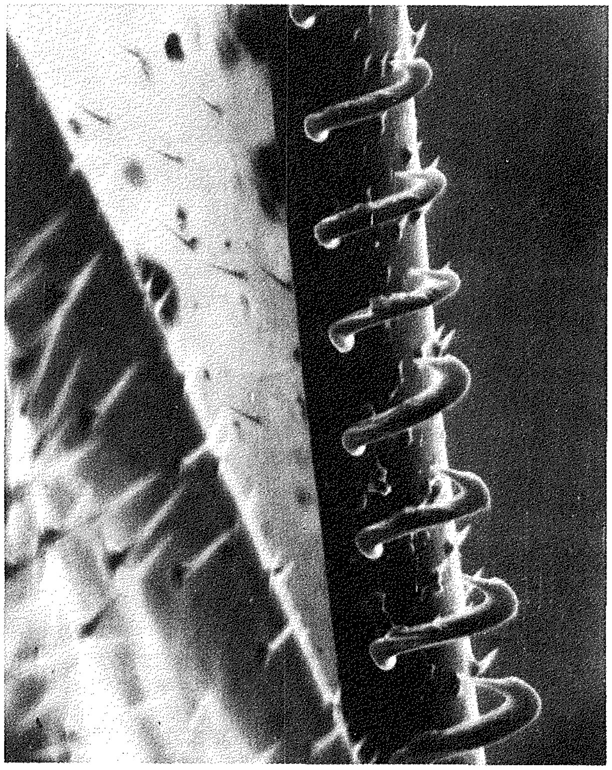


Figure 7.- Hooks present at the edge of the posterior bee wing. These hooks attach to a ridge on the anterior wing for facilitating synchronous movement of the wings during flight (ref. 24) (magnified 625 times).

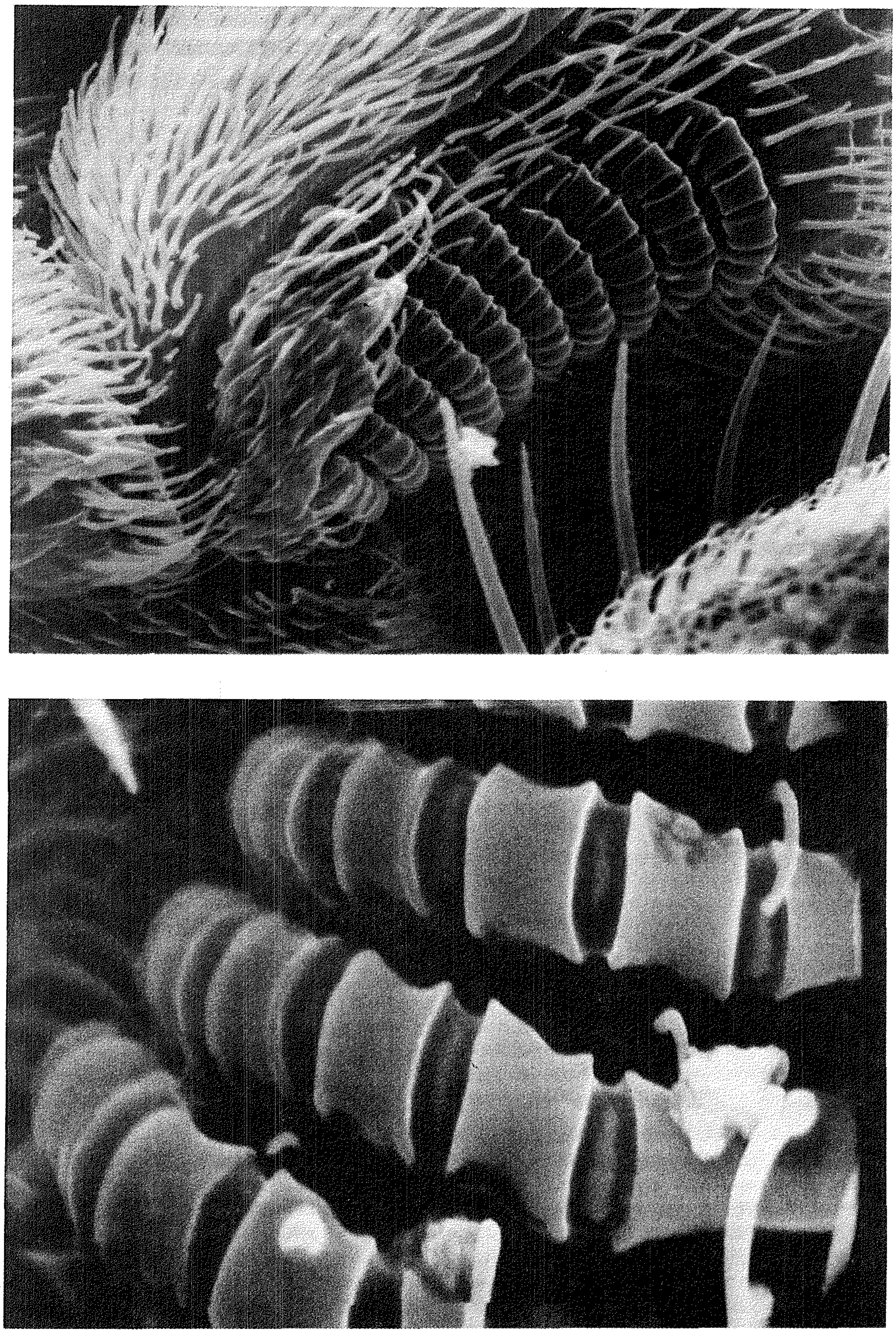


Figure 8.- High-power scanning electron micrographs of the differentiated chitinous structures of the Drosophila halteres (magnified 3000 and 7000 times).

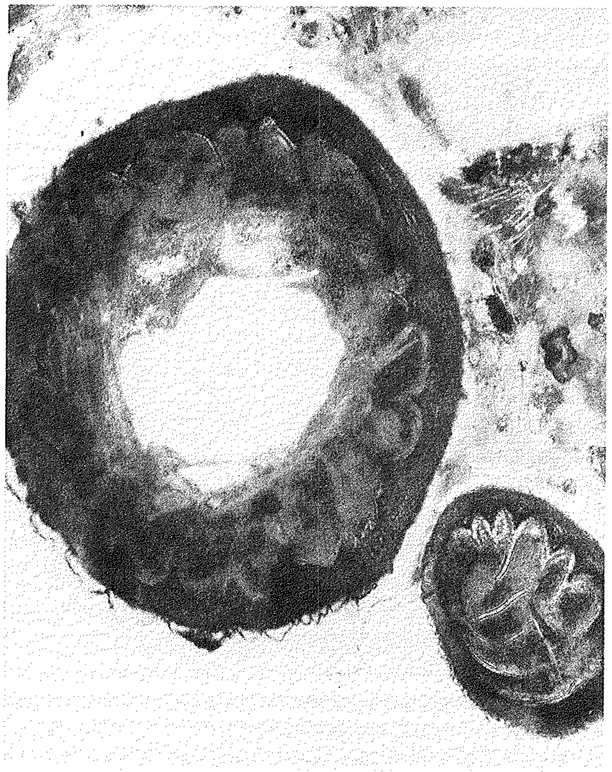


Figure 9.- Electron micrograph of the statolith-like structures found inside the halteres of Drosophila. Like the otoliths of the mammalian inner ear, these insect structures play a role in gravity and body-weight perception (magnified 12,000 times).

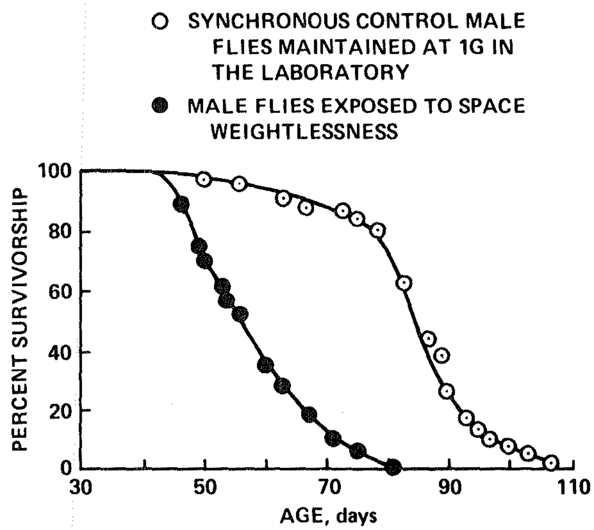


Figure 10.- When imagoes of D. melanogaster Oregon R were exposed to microgravity during about 19 days, there was a considerable life-shortening, probably because of increased oxygen utilization caused by disturbed flying behavior.

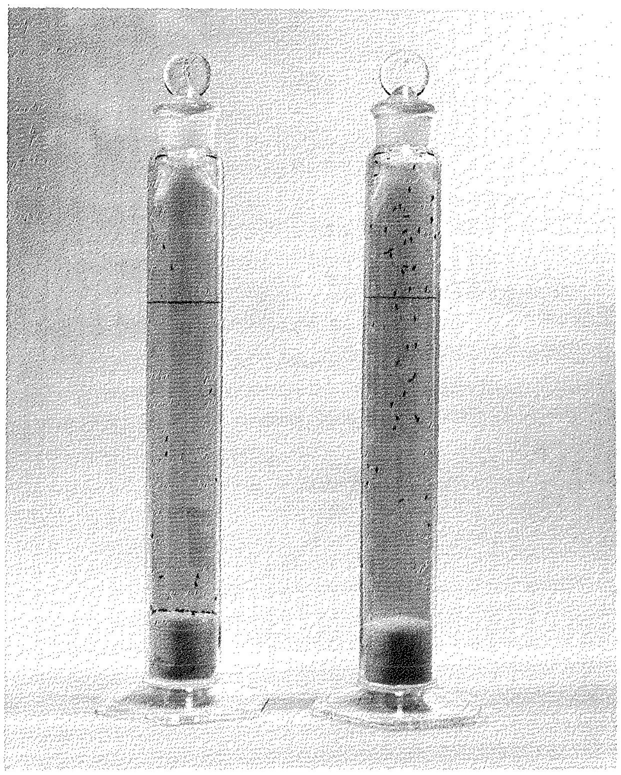


Figure 11.- Many insects show tropisms or taxis such as exemplified here (old fruit flies, left; old fruit flies, right). Some of these behavioral traits may be abolished or modified in intensity by development in microgravity.

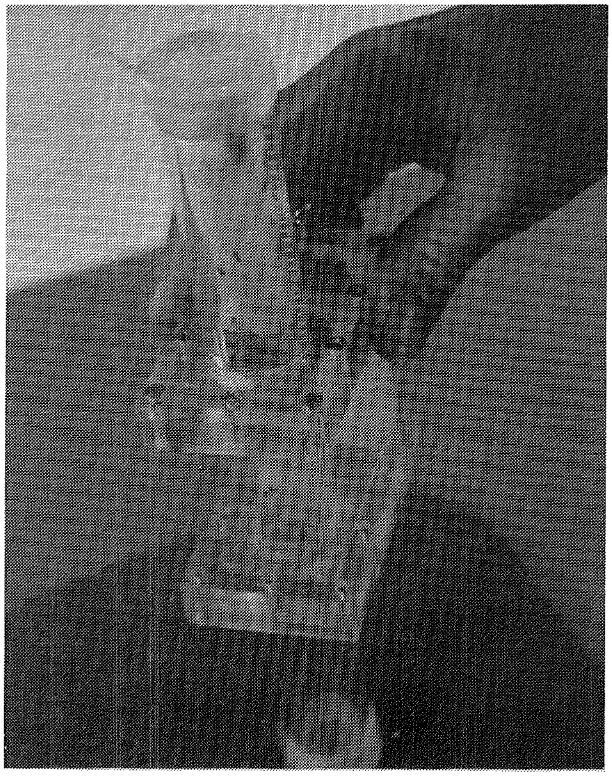


Figure 12.- Escape-proof housing unit for insect reproduction studies which has been designed in our laboratory and could profitably be used in the Shuttle Spacelab. Males are kept in the upper compartment and females in the middle compartment. After 24 hr of spaceflight the interconnecting door is opened and the flies are allowed to mate and lay eggs for 24 hr. Then the other door is opened and all adult flies and shaken and segregated into the compartment devoid of food. The eggs remain on the food and the developmental process can be studied, rendering attention to the quantitative parameters, which have been neglected in most developmental studies performed in space thus far.

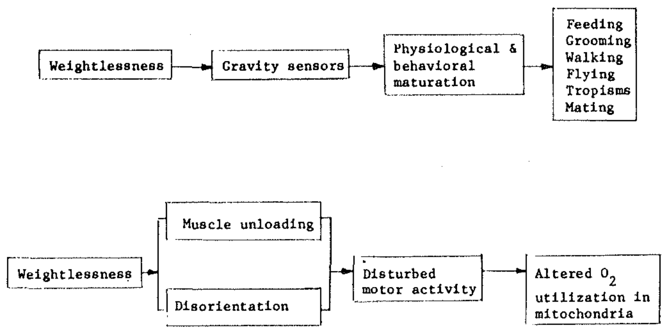


Figure 13.- The experimental data suggest that microgravity does not exert a direct effect on <u>all</u> invertebrate cells, but only on those developing cells which specialize in gravity sensing. This postulated effect of microgravity may affect the behavioral maturation of the animals, with concomitant alterations in metabolism and behavior.