

Photograph by R. E. Crabill, Jr.

ROBERT EVANS SNODGRASS (1958)

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MORPHOLOGY

PUBLISHED IN HONOR OF DR. ROBERT EVANS SNODGRASS
ON THE OCCASION OF HIS EIGHTY-FOURTH BIRTHDAY
JULY 5, 1959

Robert Evans Snodgrass



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FOREWORD

It is with a great deal of pleasure that the Smithsonian Institution publishes this volume of original contributions in honor of Dr. Robert Evans Snodgrass. Dr. Snodgrass is universally acknowledged to be among the foremost insect morphologists of our time, and his scholarly and painstaking work in his field has won for him the admiration and respect of his colleagues throughout the world. This feeling is expressed in one way or another by each of the authors of the papers specially written for publication in this volume.

Although Dr. Snodgrass has never been on the active staff of the Smithsonian, nevertheless he saw fit as far back as 1919 to offer the results of his researches to the Institution for publication. The Institution on its part was more than willing to undertake their publication, for original researches and the publishing of the results thereof constitute one of the principal means by which the Smithsonian implements James Smithson's mandate for "the increase and diffusion of knowledge among men."

The arrangement has continued up to the present time, and over the years the Institution has published in its Miscellaneous Collections series a large number of Dr. Snodgrass's scientific contributions, as well as several popularized papers on insects in its Annual Report Appendixes, which are intended to foster an interest in science among the general public. An assessment of the significance to science of these contributions will be found in the biographical sketch appearing elsewhere in this volume.

In 1953 Dr. Snodgrass was appointed an Honorary Collaborator of the Smithsonian Institution, which title he continues to hold to the present time. At the age of 84 he is actively engaged in further research in his field, and it is hoped that many more of his basic contributions to insect morphology will appear under the Smithsonian imprint.

LEONARD CARMICHAEL
Secretary, Smithsonian Institution

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ROBERT EVANS SNODGRASS, INSECT ANATOMIST AND MORPHOLOGIST

By ERNESTINE B. THURMAN¹

Adversity is seldom dull. The things we do in this world do not count for half so much as those that happen. I would not exchange the unexpected in my life for all that I've achieved through efforts of my own. The events we set in motion by pre-conceived design take us along conventional routes that we expect will lead on to success, while those that fate ordains create all the diversity and give all the excitement that make it worth while to live.

R. E. SNODGRASS, 1914 (unpublished diary).

The author of this biography accepts with pleasure the unexpected privilege and honor of being invited to participate in offering this well-deserved tribute to Dr. Robert Evans Snodgrass, on this rare occasion, his 84th birthday. There are many throughout the world who join in expressing best wishes and felicitations, and who share the author's sentiments of appreciation, admiration, and respect for so eminent an entomologist.

Dr. Snodgrass is one who, after more than half a century, still is rendering distinguished and inestimable service to mankind through his contributions to the science of arthropod morphology, anatomy, evolution, and metamorphosis. He is known and admired by many as a friend, a teacher, an author, a literary critic, and an artist, as well as a savant and an internationally renowned scientist. It is difficult to separate his sterling qualities of character and his innate talents for drawing and writing, so well known to his students and colleagues, from his scientific accomplishments which are the result of an insatiable quest for scientific truths and a remarkable ability to observe and interpret.

All these attributes are harmoniously composed into a dignified, erect, gracious, unassuming gentleman of remarkable health, agility, and strength who is possessed of a profound depth of philosophy, a sparkling sense of humor, and a vigorous zest for living. This is a

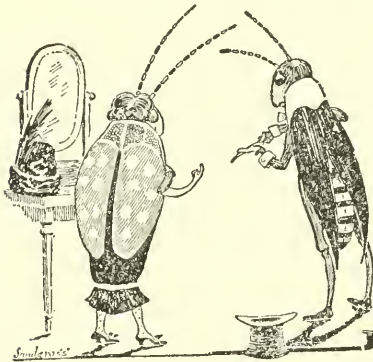
¹ Senior Scientist (R), Medical Entomologist, Division of Research Grants, National Institutes of Health, Public Health Service, Department of Health, Education, and Welfare, Bethesda, Md.

composite which is the dream of countless men many years his junior, but realized by few. A thick shock of glistening white hair, a ruddy complexion, and alert blue eyes, which require the aid of glasses only for reading, denote unusual physical stamina. A phenomenal memory for facts and events, a wealth of basic knowledge at his ready command, thorough training in the use of the Classical and Romance languages, and an unlimited vocabulary in English and German, spiced with wit, which is ready but sometimes sharp, make conversations with him informative and memorable pleasures.

The author has spent many enjoyable hours listening to Dr. Snodgrass relate incidents of his early life, reading his unpublished diary and travelogs, browsing through his correspondence files and publica-

tions, laughing over original copies of his cartoons, and admiring his numerous precise drawings and oil paintings of insects and their life histories, which are accurate in minute detail as well as being noteworthy as works of art.

"My ancestry is as unknown to me as I am to my ancestors, but I believe I am a typical American, since, judging from the family names, I must be a mixture of English, Scotch, Welsh, and Irish, and I do not know who my grandfather was." (His sister belonged to the Daughters of the American



"COME, DEARIE, BE A GOOD BOY, NOW, AND
HOOK UP MY SHELL BEHIND FOR ME."

(From *Life*, Feb. 23, 1911.)

Revolution.) Thus, Dr. Snodgrass opened one conversation with the author, continuing with the information that his parents, James Cathcart Snodgrass and Annie Elizabeth Evans Snodgrass, came from Ohio and settled in St. Louis, Mo. There he was born on the 5th of July, 1875, so they told him. A sister and brother, born 3 and 8 years later, completed the family. He lived in St. Louis until about the age of 8 years.

His first ambition in life was to become either a railway engineer or a Pullman conductor, but he could never decide which personage looked more important. Before leaving St. Louis, however, an interest in zoology had been aroused through visits to the St. Louis Zoo. There the sea-lion in particular so impressed him that he became adept in imitating its manners and bark, much to the consternation later of one of his mother's friends. His mother, while entertaining a lady

guest one afternoon, stepped into the kitchen for a moment. Young Robbie (as he was known then), left alone with the lady, felt it his duty to entertain her. Throwing himself onto the floor directly in front of her, ventral side down, he proceeded to give his best impersonation of the sea-lion, raising himself on his front flippers, stretching up his neck, and barking while swinging his head from side to side. The lady unaccountably became pale and rigid, got up, went to the kitchen door, and in a tremulous voice said, "Mrs. Snodgrass, I think there is something the matter with your little boy." His mother relieved her with the information that he was only playing sea-lion, but the lady did not ask for an encore.

The first entomological observation which Dr. Snodgrass recalls is seeing that the legs of grasshoppers, cut off by his father's lawn mower, could still kick while lying on the pavement. This apparently mysterious fact made a strong impression on him, and he decided that sometime he would look into the matter.

In 1883 the Snodgrass family moved to the town of Wetmore in northeastern Kansas, where his father became a cashier in the bank, later rising to higher offices. Here Robbie's interest turned to machinery, and he finally made a steam engine that almost worked—the piston would go out but it would not go back. However, the turning point in his life came when he received an air gun and target as a birthday gift. Though shooting at a target soon became rather tame sport, the family principles absolutely forbade the shooting of birds. Then an inspiration saved the situation; he would learn to mount birds and thus preserve them for science. This argument prevailed to the extent that he was allowed to shoot two birds of each kind. So he obtained a small book, "Taxidermy Self-taught," and soon had a vacant bookcase full of birds sitting on perches, looking rather uncomfortable, but still giving a fair imitation of how they appeared in nature. Then he became known locally as a professional taxidermist. When pets in the neighborhood died, the owners brought them to him for mounting. Their appreciation, however, usually was expressed in such remarks as, "No, Dickey never did look like that," or "Polly didn't have shoe buttons for eyes." This discouraged him from following taxidermy as his life's work. Accordingly he decided to be just an ornithologist, and continued to shoot and mount birds for his own collection. His efforts were rewarding, as some of the specimens were borrowed once for exhibition at a local county fair. It must be understood, of course, that there were no Audubon Societies in those days, and that field-glass study of birds was yet a long way off. Only a bird in the hand could be identified. Later he acquired Coues's "Key

to North American Birds" (which he still has), and then prepared specimens as museum-type skins.

After 7 years in Kansas the family moved again, this time to southern California, where they finally settled on a 20-acre "ranch" in Ontario, planted to oranges, prunes, and grapes. In Ontario the 15-year-old Snodgrass (called Rob at this age) entered a Methodist preparatory school of high-school level, then known as Chaffey College. Here he studied Latin, Greek, French, German, physics, chemistry, and drawing, but no biology which might involve evolution. On the side, however, he read Darwin, Spencer, and Huxley, thereby becoming branded as a heretic. His interest in anatomy now was awakened and he spent Saturdays, and Sundays after church, dissecting birds, cats, frogs, crayfishes, and other animals. Notes and drawings from these endeavors provided entrance credit in zoology when he later went to Stanford University. But his openly avowed belief in evolution estranged him at home and caused him to be expelled from Sunday school, much to his satisfaction.

In 1895, at the age of 20, Rob Snodgrass entered Stanford University and majored in zoology. The whole atmosphere now was changed. He had excellent courses in general zoology, embryology, and comparative vertebrate anatomy. From Dr. David Starr Jordan, who was then president of Stanford University, he of course learned something about fishes. It seemed to him, however, that nearly everything must already be known about vertebrate animals, so as a side course he took entomology under Prof. V. L. Kellogg. Soon Professor Kellogg set him to work on the anatomy of the Mallophaga—biting-lice, a group in which the professor was specializing at the time. The prospect of doing original work that might even be published inspired Snodgrass to acquire a new outlook on life and provided the impetus for investigations from which came his first two publications (1 and 2),² "The Mouth Parts of the Mallophaga" (1896) and "The Anatomy of the Mallophaga" (1899). The long-cherished dream of being an ornithologist was given up.

While a student at Stanford University, Rob Snodgrass had two interesting and profitable trips. The first took him, as one of a party selected by Dr. Jordan, to the Pribilof Islands to study the habits of the fur seals. At that time a dispute involving other countries existed over the right to kill seals in the ocean. The second was a 10-month trip with Edmund Heller to the Galápagos Islands in a 100-ton sailing

² Numbers in parentheses refer to the Snodgrass bibliography that follows this paper.

schooner, the *Julia Whalen*, with Captain Noyes of San Francisco in command. They visited all the islands of the eastern Pacific from California to the Equator. The crew included the captain, the mate, three sailors, and the cook. Their principal objective was the skins of the southern fur seals. Life on a small schooner in those days was primitive and monotonous compared with that on a modern luxury yacht. The staple diet was salt beef and hardtack, except when at anchor. Then fish and even sea turtles were obtainable. Although ocean currents continued their movement, the wind did not always blow when wanted. As a result much time was lost in attempts to arrive at specific points, but the expedition eventually visited every



THE ORDER OF THE BATH

(From Judge, Nov. 28, 1914.)

island of the archipelago. Heller and Snodgrass collected everything from giant tortoises to bird lice, in addition to plants and samples of lava, but specialized on birds, insects, spiders, and fishes.

The Galápagos Islands, though on the Equator, are not a tropical paradise. They are of volcanic origin with much of their surface consisting of raw lava. Only one of the islands gets enough rainfall to permit cultivation. In his account, Dr. Snodgrass stated that walking over newly cooled lava beds makes one feel like a spider or an ant traversing a cinder path, and that getting to the top of a 3,000-foot crater is a strenuous day's exertion. Before the party left the islands, one volcano came to life and gave a brilliant exhibition. It is fortunate that accidents did not occur, as any kind of accident could have been serious without medical care. Though hungry ticks were abundant and

mosquitoes swarmed in the rainy season, on the islands that were without human inhabitants there were no diseases for the arthropods to transmit.

Zoologically the archipelago is noted for the differentiation of species on the different islands. Collections from the trip went to Stanford University and were distributed to specialists whose papers were published in the Proceedings of the Washington Academy of Sciences and other journals. Snodgrass individually or with Heller authored seven papers (3, 5, 6, 7, 12, 16, and 19). Edmund Heller became a noted collector of mammals and later accompanied Theodore Roosevelt on his African Expedition.

In 1901 Robert E. Snodgrass was graduated from Stanford University with an A.B. degree, and took a teaching job at the State College of Washington in Pullman under Prof. C. V. Piper, an enthusiastic entomologist and botanist at that time, later an agrostologist in the U. S. Department of Agriculture. During the summer vacations Snodgrass, with two companions, two horses, a wagon, and camping equipment, explored the central desert of the area, then as nature had left it, and traversed the Grand Coulee before it was "dammed by a dam."

After 2 years at Pullman, he returned to Stanford University as an instructor in entomology under Professor Kellogg. Here he made his first acquaintance with honey bees in an observation hive. This initial interest was sustained and led to his intensive studies of honey bees (23, 50, 76). During the period at Stanford (1903 to 1905) he added 11 publications (9 to 19) to his rapidly lengthening bibliography. However, it seems that the authorities were not too pleased with the young instructor, mainly on minor accounts. For one thing, Professor Kellogg was in Europe, and in his absence it was the duty of Snodgrass to feed some newly hatched silkworms in the laboratory. The larvae, of course, had hatched ahead of the season outdoors, and vainly he searched the campus for mulberry leaves. (This was before it was known that the larvae would eat lettuce.) At last he found a single tree with young leaves, climbed the tree, picked the leaves, and saved the lives of the experimental silkworms. The tree, however, refused to put out more leaves and inconsiderately died. It was in a row of shade trees in front of the men's dormitory, and thus rated in importance ahead of silkworms. After some other minor indiscretions of a similar nature, Snodgrass went to San Francisco, jobless, to brush up on his drawing.

In San Francisco he obtained a job in the art department of an advertising company and attended an art school at night. He did

some magazine covers, designs of clay-modeled animals, and was to be taken on the staff at the San Francisco Academy of Sciences. However, the morning after he had been accepted by the Academy, the earthquake of 1906 shook up things, and then the fire came. He was living at the time south of Market Street with Sidney Peixotto, brother of the artist Ernest Peixotto, and several young men associated with him in a boys' club. Directly across the street was a large playground. After the earthquake shock, which left the house still standing, they all moved into the playground with whatever they could salvage. (All Snodgrass's possessions were contained in one trunk.) Here, with a large crowd of other refugees, they lived in an improvised shelter while everything surrounding them was in flames. After several weeks of "camping out," Snodgrass packed his trunk and went home to Ontario for the summer.

In the fall of 1906 he cashed an insurance policy in order to go to Washington, D. C. Dr. L. O. Howard, then Chief of the Bureau of Entomology, U. S. Department of Agriculture, took him on the staff at a salary of \$60 a month, and later raised it to \$100. During the next 4 years in the Bureau he produced 5 more publications (20 to 24). Dr. E. F. Phillips, then Head of Apiculture, gave him the opportunity to do his first work on the anatomy of the honey bee.

By the summer of 1909 he had a bank account of about \$300 and decided to take a trip to England and Scotland. This being in the days before passports and accumulated leave, he was granted a 3-month furlough from the Bureau. He purchased a round-trip ticket and took passage from Baltimore on a so-called cattle steamer. The steers, of course, traveled in the steerage and did not mix with the upper-deck passengers, who, besides Snodgrass, included American tourists, a Cambridge professor, and some prospective Oxford students. After 10 days on the Atlantic Ocean, they landed at Liverpool, and the next day Snodgrass took a train to Chester, a quaint old town with its ancient Roman wall still intact. Here he spent a week or so and made sketches of antique houses, the remains of an ancient abbey, and some other scenery.

From Chester he went north to Glasgow, where he visited a former Stanford roommate, a native of Scotland who at the time was teaching botany at the University. The friend was living just as bachelors do in Dickens's stories, with his meals served in his room by the landlady. To honor Mr. Snodgrass, the landlady served a haggis, that famous Scotch dish, which is a sheep's stomach stuffed and seasoned with too many things to inquire about, all thoroughly boiled. It was quite an experience for the American. Mr. Snodgrass and his friend

visited the home of Burns at Dumfries, Melrose Abbey, and Abbotsford, the home of Scott. Then they went to Edinburgh, a city still reeking with history, and from there to Aberdeen and St. Andrews.

Finally Snodgrass headed south for London, stopping on the way at Durham, York, Warwick, Stratford, Cambridge, and Oxford. He spent at least a month in London, traversed every section of the city on foot from a boarding house on Tavistock Square, and was disappointed only in that he did not encounter a London fog. Dr. Snodgrass, in recalling this trip, describes it as one of the most enjoyable events of his bachelor days; never before nor since has he had so much good food at a price that he could afford.

At the end of 4 years with the Bureau of Entomology, Mr. Snodgrass hinted that he might be due a raise; but Dr. Howard sadly informed him that the Department could not provide money for work in anatomy and that the only chance he now had for a raise was to change to another type of work. Thereupon he promptly resigned, again packed his trunk, pocketed his cash savings, and went to New York City.

Since cockroaches and bed bugs, then the principal insects of New York City, did not hold any particular interest for him, Snodgrass now turned to the study of the human species. He attended night classes at the Art Students' League and learned to draw the human figure. The art-school discipline of freehand drawing under a competent instructor proved to be excellent for training the eye to see form and proportions, even in an insect, without recourse to instruments. As a source of income, he composed jokes and portrayed them in pen drawings, which now and then he sold to the comic magazines of the day, such as *Life* and *Judge*; also he did a few more serious illustrations. As a pastime, he made pencil sketches of New York's interesting street scenes, but the latter have changed considerably over the past years.

The life of an artist he found delightful—no hours to keep, get up when one pleases, stay up all night if one wishes to study night life, no responsibilities except room rent. If one sometimes became short of cash, there was always the free-lunch counter, from which, by paying 5 cents for a glass of beer, enough diversified food could be had to satisfy almost any degree of hunger. Dr. Snodgrass adds, "The free-lunch counter was a great institution of the old days, but it went out with prohibition. In lower Manhattan there actually was a restaurant that served meals for 10 cents." Sometimes, in order to eat or pay his room rent, Snodgrass had to take a job in the art department of an advertising company. Here he learned much about lettering and

the practical problems of line-cut reproduction which proved to be of value to him in his future work.

When World War I was declared, things became dull in New York for artists and writers. Mr. Snodgrass accepted an invitation from an artist friend from Indiana to go with him to his native State, where he thought, with Snodgrass's assistance in selling, he could better dispose of his pictures. As business manager of the venture, Snodgrass canvassed the small towns of Indiana for customers, and at least met many interesting people. Also he was able to observe the Hoosier in all his local color. So, while his friend frantically slapped color onto his canvases to supply orders, Snodgrass sketched the more picturesque Hoosiers, depicting their everyday life and manners. It would appear from his sketches that the males of the day were chiefly remarkable for growing whiskers, loafing in groups according to age and length of beards, chewing tobacco, and distance and accuracy in expectoration; the females for cooking, rearing large families, and acquiring physiques that looked like feather pillows tied in the middle.

The venture in selling paintings was interesting but financially not particularly successful. So one day Mr. Snodgrass casually

dropped into the office of the State entomologist in Indianapolis, and unexpectedly was invited to join the staff. Here again was demonstrated the value of events that happen by chance.

Again he found himself in entomology. Frank Wallace soon became head of the office. Harold Morrison and Harry Dietz were in the midst of preparing their book "The Coccidae or Scale Insects of Indiana," and wanted an artist for the illustrations. Through outdoor work and contact with the farmers and their problems, Snodgrass learned much about practical economic entomology. He also wrote "Some of the Important Insect Pests of Indiana" (25) and made oil-painting wall charts of farm and garden insects.



"Unnecessary advice." R. E. Snodgrass.

(From Indiana sketch book, 1916, unpublished.)

After two entomologically profitable years in Indianapolis, Mr. Snodgrass in 1917 decided to try his luck again in Washington, D. C., where he offered as an inducement his newly acquired chart-making abilities. This appealed to Dr. Howard, who once more hired him in the United States Department of Agriculture for an assignment which paid \$2,000 per year. Gradually, as the war work became less important, he again bootlegged anatomy into the Bureau and found it more in favor at that time. The entomologists seemed to want his productions, and the Smithsonian Institution accepted his papers for publication.

During these years with the U. S. Department of Agriculture, Snodgrass was assigned for several summers to work at Wallingford, Conn., where he learned much about the life histories of apple insects. Then he was transferred to a U.S.D.A. experiment station at Sligo, Md., and later to a station near Silver Spring, Md. Finally he was permanently quartered in the South Building of the U.S.D.A. in Washington, D. C.

On September 18, 1924, Mr. Snodgrass married Miss Ruth Mae Hansford, a talented musician, endowed with beauty, charm, and sparkling personality. The result, he says, is that he now has a wife, two daughters, five grandchildren, and real-estate taxes.

"The rest of my career is well known to the entomological public, and need not be detailed." In this brief statement, Dr. Snodgrass has summarized modestly his activities covering an additional 36 years of continuous research from which 54 publications (26 to 79) have been produced, and one more is in preparation.

Among the numerous recognitions of his achievements is his honorary degree of doctor of natural sciences conferred November 17, 1953, by the Eberhard-Karls-Universität at Tübingen through the interest of Prof. Hermann Weber "as Master of Anatomy and Morphology of Arthropods, in recognition of his services as original researcher, as author of fundamental books, and an example to a whole generation of morphologists." Other recognitions include his election as honorary president of the Entomological Society of Washington and honorary member of the Entomological Society of America, the New York Entomological Society, the Royal Entomological Society of London, Société Entomologique de Belgique, Société Entomologique de France, Société Entomologique d'Égypte, the Academy of Zoology of India, and the Sociedad Uruguaya de Entomología.

Throughout his career, Dr. Snodgrass has been more interested in the evolutionary changes and relationships of anatomical structures,



About this age (6 years) in St. Louis, Mo., Robbic Snodgrass made his first entomological observation, that the legs of a grasshopper cut off by his father's lawn mower could still kick while lying on the pavement.

WESTERN

FIELD



JANUARY, 1906

Magazine cover, clay model of the bighorn sheep. R. E. Snodgrass,
San Francisco, 1906.

and in describing and illustrating the morphological development of arthropod structures, than in describing new taxa of arthropods. In fact, it was by sheer accident that Dr. Snodgrass described a new species of scorpion fly, though he did not name it. He figured the structures of the male genitalia of what he thought was a well-known species of *Panorpa*. Specialists in the group assured him he had not figured a known species, but an undescribed one.

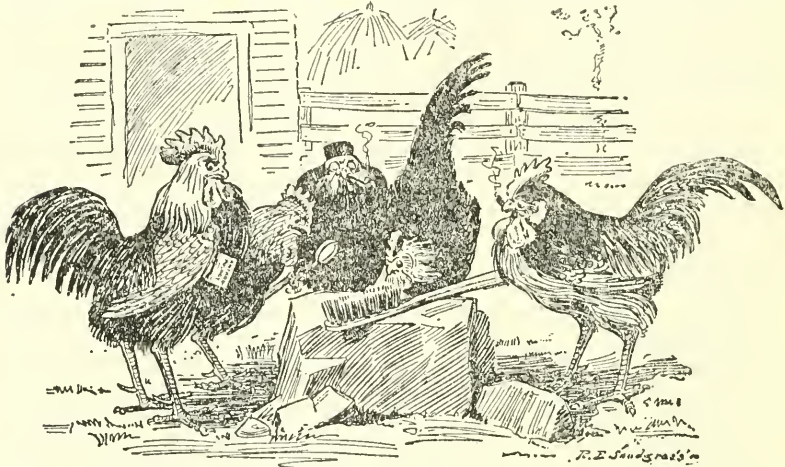
In 1945 Dr. Snodgrass reached the age of retirement. Having much unfinished work on hand, he continued his activities in space made available in the United States National Museum, space which he still gratefully occupies. Since retirement he has completed 15 publications (65 to 79), and as with all his publications, each is an important contribution in its own right. Over a period of 61 years, Dr. Snodgrass has completed 79 publications, totaling 5,972 pages and 2,154 plates and text figures, with 15 of the plates in color (44). Seldom does a plate or text figure consist of a single drawing, but more often of 10 to 15 or even 20 drawings. His bibliography exhibits both quality and quantity.

Reviews of Snodgrass publications have been exceedingly complimentary, testifying to the high regard which others have for Dr. Snodgrass and his research. About "A Textbook of Arthropod Anatomy," Dr. A. Glenn Richards (*Science*, vol. 117, p. 464, 1953) has this to say, "[Snodgrass] concerns himself with comparisons of the anatomy and terminology associated with the anatomy of the various classes of the animal phylum Arthropoda. He states the situation pungently in his preface: 'The arthropods are a group of related invertebrates; arthropodists, for the most part, are a group of unrelated vertebrates.' . . . The high caliber, the style of writing, the logical thinking, the personal verification of most of the details presented—even when they are credited to a previous author—and the many superbly drafted illustrations (very few of which are copied) are typical of the author's work."

Of the same book, Dr. V. G. Dethier's review (*Quarterly Review of Biology*, 1954, p. 179) includes these statements: "An outcome of a lifetime of study of insect structure and ancestry . . .," "a masterful piece of work, clearly presented, and attractively printed," and "a profusion of excellent illustrations which has come to be associated with all Snodgrass' works."

In his review of the "Anatomy of the Honey Bee," Dr. Roland Walker (*Science*, Oct. 19, 1956) uses such phrases as "precision and elegance of the pen work . . .," "constant evidence of Snodgrass' critical judgment . . .," and "the labels punctiliously revised to con-

form to changed concepts of homology." In a review of the same book, Dr. R. G. Schmieder (*Entomological News*, vol. 67, No. 9, pp. 250-251, 1956) quotes the beginning of chapter II, "An insect is a living machine; no other animal is provided with so many anatomical tools, gadgets, or mechanisms for doing such a variety of things as a winged insect." Dr. Schmieder describes Snodgrass as having "gone over carefully the mountains of recent literature with all its detailed



A MEETING OF THE SCIENTISTS TO DELIBERATE ON THE POSSIBLE USES OF AN INTERESTING DISCOVERY.

(From Chicago Record-Herald, 1913.)

data and has boiled down and refined all its profusion and confusion to the basic essential facts which he presents with amazing clarity and simplicity. . . . This is not a technical reference book; [it is] essentially a treatise on entomology, using one species as an example and including a discussion of the fundamentals . . . [it] can be read straight through with pleasure . . . a delight to follow the author through this complete examination of one insect. . . ."

One of the most delightfully illustrated works of Snodgrass is "Insects, Their Ways and Means of Living" (44). The colored plates, numbering 15, are reproductions of oil paintings, some of which today grace the wall of the Snodgrass office, and of water-color studies, some of which Dr. Snodgrass has given to entomologist friends. One edition is beautifully bound, with pages edged in gold, befitting the careful and detailed studies contained therein. This book exemplifies a rare talent, the ability of a specialist to present a technical subject com-

pletely accurate in detail in a style which can be read and appreciated by both specialists and laymen. Dr. Snodgrass's continued study of evolution, for which he was branded a heretic in 1894, is evident in his discussion of the Diptera. "Scientifically, the Diptera are most interesting insects, because they illustrate more abundantly than do the members of any other order the steps by which nature has achieved evolution in animal forms. An entomologist would say that the Diptera are highly specialized insects; and as evidence of this statement he would point out that the flies have developed the mechanical possibilities of the common insect mechanism to the highest general level of efficiency attained by any insect and that they have carried out many lines of special modification, giving a great variety of new uses for structures limited to one mode of action. But when we say that any animal has developed to this or that point of perfection, we do not mean just what we say, for the creature itself has been the passive subject of influence working upon it or within it. A fundamental study of biology in the future will consist of an attempt to discover the forces that bring about evolution in living things."

"Principles of Insect Morphology," published in 1935 (53), is considered by many to be the masterpiece of Snodgrass. It is described by Dr. Hans Sachtleben (Deutsches Entomologisches Institute, vol. 3, pp. 676-677, 1953) as the "greatest work." Dr. Clarence Hamilton Kennedy (Science, vol. 83, pp. 413-415, 1936) deemed this text to be "a volume of interest to zoologists as well as to entomologists." Dr. Kennedy acknowledged the abilities of the author and noted the careful writing of the book, that it is not just an expansion of lecture notes into chapters. "It is this remarkable ability to see things, then to draw them in a superb style that makes an outstanding anatomist . . . [the] ability to see the riches in the common and abundant, to organize and interpret the commonplace is one of the characteristics of a genius. . . ." And so for more than 20 years "Principles of Insect Morphology" has been and still is the leading text dealing with insect structure. Copies have been printed in numbers approaching 9,000 for the use of students and specialists throughout the world.

In explaining the difference between "anatomy" and "morphology," Dr. Snodgrass tells us that "anatomy is what you see with your eyes, morphology is what you *think* you see with your mind." The recorded facts of anatomy, he points out, do not change much with the years; but morphological concepts vary according to the mental vision of the morphologist. The zoologist, however, should continually revise his morphological outlook as new facts come to light. Through the years a few students of morphology have not agreed fully with the morpho-

logical concepts of Snodgrass, evidently owing to the understandably different mental interpretations by the individuals.

Dr. Snodgrass's contributions to science have not been confined to his printed pages. He has given and still is giving freely of his time and technical resources in guiding the efforts of others through personal direction or through correspondence. Students have traveled thousands of miles for the privilege of working under the guidance of Dr. Snodgrass. It is the customary thing to find references by Snodgrass listed in the bibliography of almost every publication dealing with arthropod morphology and anatomy, evolution and metamorphosis, and embryology. In these and publications treating other fields of entomology, illustrations marked "after Snodgrass," "following Snodgrass," "courtesy of Snodgrass," or "R. E. S." are numerous. Students in unrelated fields often request and receive assistance from Dr. Snodgrass. Currently a young journalist who was inspired by the delightful treatment of aphids in "Insects, Their Ways and Means of Living" (44) is writing an account of the life of an aphid, being privileged to use the prized illustrations signed "R. E. S."

As a lecturer, "Professor" Snodgrass is often in demand. He is a clear and concise speaker with the ability to present a complex subject in a simple and entertaining manner. Well known to his audiences is his talent for adroitly sketching illustrations on the blackboard. Dr. Snodgrass was a special lecturer in entomology at the University of Maryland from 1924 to 1947. Since then he has given lectures at the University of Minnesota, Cornell University, and the University of Virginia in addition to continuing as guest lecturer at the University of Maryland. He has the ability to increase the number of listeners with each lecture as a series progresses.

During the 1957 series at the University of Maryland, the lectures were attended by students and professors from other departments and colleges on the campus in addition to the Department of Entomology, from neighboring institutions, and from adjacent cities. The current students often found it difficult to keep up with the Snodgrass pace of lecturing and illustrating. Students of former years report that in their day Professor Snodgrass spoke and sketched even more rapidly than today; the sketches, then as now, did not require any retouching; and the only way they could equal the pace was to work in pairs, one copying and labeling the sketches while the other wrote the lecture notes. Professor Snodgrass admits that in those days perhaps he did occasionally sketch with a piece of chalk in each hand.

In keeping with his rapid, precise thinking and sketching, Dr. Snodgrass writes quickly, "just as the thoughts come to me." Then he



Calton Hill cemetery and prison, Edinburgh, Scotland. R. E. Snodgrass,
Nov. 1909.
(From collection of unpublished sketches.)

polishes his manuscripts with a few easy changes in one or two rewrites, not having to undergo the laborious task of rewriting numerous times as the majority of us do in our scientific literary endeavors. With a chuckle, Dr. Snodgrass mentioned one reason for his not rewriting manuscripts—Mrs. Snodgrass does not like to retype the papers.

Concurrently with his lecturing at the University of Maryland, he generously supervised thesis research for graduate students, each student receiving meticulous and inspiring guidance. The published investigations of these students have added much to the knowledge of insect anatomy and morphology. The accomplishments of these students, who are specialists today, testify to the abilities of their instructor.

Dr. Snodgrass has always been an avid reader who enjoys a wide variety of subjects and authors; and routinely reads for hours every night. His favorite of all books is that most humanized animal story, "The Wind in the Willows," by Kenneth Grahame (1908). It is in keeping with the simplicity of Dr. Snodgrass's innate interest in and fondness for animals—an intrinsic part of his personality which has been revealed in many ways.

When the author inquired of Dr. Snodgrass if he were a sports fan or a hobbyist, he answered in the negative. A few minutes later he brought to her desk two pages of notes, quickly written in the usual Snodgrass style, treating his lack of interest in hobbies and sports. Here they are just as he initially wrote them.

PERSONAL NOTES

"I never have had any hobbies, and have given little time to pure recreation. While I have played tennis a little, golf has always seemed too much of a gentleman's game. I used to like circuses because they had animals, but theaters to me are only something you have to take girls to before you get married. However, I do enjoy window shopping to see how many thousands of things there are that I don't need and don't want. In my youth I had plenty of involuntary exercise sawing the family stovewood and mowing the lawn. Later, on my own volition, I did a good deal of long-distance hiking, and some mountain climbing where mountains of reasonable height were easily available. But at school I was no good at all in athletics, except in running games. In fights I always got the worst of it, and thus became a popular victim. In baseball I was a complete failure; the ball either made a bee line for my face, or if it did hit my hands, it had a trick

of bouncing back before I could close my fingers on it. In the classroom I excelled principally in copying maps and in making those analytical diagrams of sentences by which we learned grammar in my early days at school (and in drawing pictures of the teacher).

"Life in general has been enjoyable, though it took me about a year to get used to it. At present my principal dislikes are barking dogs, radios, getting up in the morning, and nutmeg in apple pie. My only regrets are the things I didn't do. If I have had any enemies they have gone where they deserve to be. Since my only physical disability is dental, I expect to live as long as I can eat—if the price of food doesn't go too high. When I die I hope to be cremated because I still retain a dread of possible resurrection and the Judgment Day.

"This is just a brief sketch. It does not include all that I remember, or anything I have forgotten.—R. E. S., April 8, 1957."



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CONTRIBUTIONS TO THE PROBLEM OF EYE PIGMENTATION IN INSECTS: STUDIED BY MEANS OF INTERGENERIC ORGAN TRANSPLANTATIONS IN DIPTERA

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(WITH ONE PLATE)

INTRODUCTION

The biosynthesis of the brown eye pigment in insects has been elucidated especially by the well-known studies of Beadle, Ephrussi, and Tatum on *Drosophila* (see Wagner and Mitchell, 1955), and of Kühn and his school on *Ephesia* (see Kühn, 1955). One of the essential facts revealed by these investigations is the occurrence of "diffusible substances" in the blood of the immature insect. These substances are pigment precursors, which are produced not only by the prospective eye tissue but also by other organ tissues. Because of these findings it has been possible to introduce by organ transplantation pigment precursor substances into the organic environment of the developing insect. Eye mutants lacking the brown eye pigment could thus be provided with appropriate pigment precursors and the differentiation of the brown eye color analyzed. By the use of this and other methods it was finally shown that the diffusible substances were intermediate compounds of tryptophane metabolism. A metabolic map for the formation of the brown eye pigment could be constructed, showing that the metabolic events led from tryptophane to formylkynurenine, kynurenine, 3-hydroxykynurenine to the brown pigment. In the many eye-color mutants investigated, genes have been found which block this biosynthetic chain at different points. The responsible genes most interesting in this connection are those that block the formation of diffusible intermediates. One gene prevents the transformation of tryptophane into kynurenine, and one other renders impossible the conversion of kynurenine into 3-hydroxykynurenine. Thus, in a mutant lacking the brown eye color because of the genetic block involving the first gene, color development can be restored by the transplantation of an eye primordium from a normal wild-type donor. The trans-

plant supplies to the blood of the mutant host the necessary precursor substance in the presence of which the pigment synthesis can be completed. Injection of the pure precursor, in this case kynurenine, also restores pigment formation. The genetic evidence, however, suggests that there are after 3-hydroxykynurenine two further steps before the final pigment is formed. The corresponding intermediate compounds are not known and they are apparently also not diffusible.

Since most of the experiments involving the transplantation technique as a tool for the analysis of eye-color development in flies were performed on *Drosophila*, it was of interest to know whether the same metabolic pattern also holds for other Diptera. The occurrence of two eye-color mutants, one in our *Musca domestica* and the other in our *Phormia regina* culture, provided the experimental material for such a comparison. The eye color of these two mutants is a yellowish green, strikingly distinct from the reddish-brown eye color of the wild-type flies. It was soon established that the development of the brown pigment in the green-eyed mutant depended on a diffusible intermediate, for the eyes of both green mutants on transplantation into a normal wild-type host developed an eye coloration that approximated the color of the wild-type host. It was also found that other wild-type genera elicited the diffusible precursors needed for the development of pigment in the eyes of the green mutants. All the experimental evidence reported in this paper, based on transplantation of organs between different genera, on injections of pure pigment precursors, and on observations of testis pigmentation suggests that the biosynthesis of the brown pigment in *Musca* and *Phormia* is very similar to that found in *Drosophila* and other insects.

MATERIAL AND METHODS

The experimental material used for these investigations includes the following Diptera: *Musca domestica* (Linn.), *Musca domestica* mutant green, *Phormia regina* (Meigen), *Phormia regina* mutant green, *Callitroga macellaria* (Fabr.), *Fucellia maritima* (Haliday), *Cynomya cadaverina* (Fabr.), and *Sarcophaga bullata* (Parker). The majority of the experiments were performed on *Musca domestica* and *Phormia regina* and their two green-eyed mutants. The eye color of these two mutants is very similar: it is a yellowish green. The eye of the *Phormia* mutant is perhaps a little more yellow. Both mutant stocks, if raised on meat, produce in mass culture flies with remarkably uniform eye color.

Last-stage larvae, shortly before puparium formation, were used

for all experiments. This stage is easily recognized because the larva empties its gut before forming the puparium. Larvae in which the gut was almost or completely empty were selected for the operations. Such larvae need not be fed. They were kept, according to the size of the species used, two to four individuals together in small screw-top glass vials (2.5×6 cm.) containing a strip of filter paper, at 25°C. room temperature.

The organ transplantations were made with a *Drosophila* injection apparatus (Bodenstein, 1950). The desired organ discs or other larval tissues were simply injected into the body cavity of the host larvae. The organ discs of large donor species were sometimes cut in half before they were transplanted. When *Musca domestica* was used as host, the mortality following the operation was very low. Usually up to 80 percent of the animals survived. In some series a 100-percent survival rate was recorded. But not all the species used as hosts withstood the operation this well. These cases will be discussed in the appropriate place in the text. No special effort was made to quantitate the amount of eye or testis pigment produced. Cases in which eye-color changes occurred were recorded as positive, regardless of the magnitude of the change, but it must be emphasized that the color change in such positive cases was always clearly noticeable. In some experiments an effort was made to grade roughly the observed eye-color effects as strong, medium, weak, and none. Strong represents an effect in which the color density almost resembles that of a normal wild-type eye.

The 3-hydroxykynurenine used in these experiments was prepared and made available to us by Dr. Peter Karlson (Münich, Germany). I am very grateful to him for his kindness in supplying this material, especially since the commercially obtained compound proved to be unsatisfactory. I would also like to acknowledge here my deep appreciation to Dr. Karlson for many helpful suggestions and for his stimulating discussions concerning the problems dealt with in these communications.

EXPERIMENTAL

TRANSPLANTATION OF EYE DISCS BETWEEN WILD AND GREEN-EYED MUSCA

When the eye disc of a wild *Musca* larva is transplanted into the body cavity of the same type host, the transplant, on the emergence of the host, is developed to imaginal completion and shows the same coloration as the eye of its host—i.e., that of a wild-type eye. When

the eye disc of a green *Musca* larva is transplanted into a green larval host, its imaginal color characteristics are also maintained—i.e., they are those of a green-eyed fly. The color development of a wild *Musca* eye disc is also autonomous when transplanted into the larva of a green *Musca* host. Fifty-nine flies bearing such grafts were available for study, and in all, the coloration of the transplant was of the typical donor type.

In 44 of these cases in which each host had received one-half or one eye disc, the modification of color in the mutant eye was slight and variable, with the exception of one in which the transplanted disc was very large. The color of this host eye was almost that of a wild-type eye. While removing the transplanted eyes from the adult flies, one gained the impression that the amount of eye pigment produced in the host was related to the size of the graft. The larger the graft the more color appeared in the host eye. If this inference is correct, much more heavily pigmented host eyes were to be expected after the transplantation of two eye discs together into the same host. Accordingly, such an experiment was designed; it consisted of 15 successful cases. A strong effect of the two-eye grafts on the color of the host eyes was clearly demonstrable. Seventy-three percent of the hosts showed the effect. Although the strength of the effect varied somewhat among individuals, the overall intensity of the eye-color change was greatly increased in this series as compared with the effects observed in the "one-eye graft" series. One can conclude that a genetically green host eye can be changed toward wild-type coloration by the transplantation of wild-type eye discs. The transplanted wild disc must have released into the blood of the host a diffusible substance necessary for pigment formation in a green eye. The amount of pigment formed apparently depends upon the amount of substance released—i.e., on the size of the graft.

The dependence of the mutant green-eye tissue for pigment development on a substance released by the wild host eye has been further substantiated by the results of the transplantation of green eye discs into wild-type host larvae. In such a combination, of which 39 cases are available, the green-eye implant gives rise to a pigmented eye almost indistinguishable from a normal wild-type eye implant. The variations in color intensity in the green host eyes observed after transplantation of wild-type eyes do not occur in this series. On the contrary, the eye pigmentation of all the implants is uniform. The substance (or substances) responsible for this effect is apparently produced in the wild host in such quantities as to allow for the maximum pigment development of which the transplant is capable.



Parabiosis between white-eyed (left) and black-eyed (right) *Periplaneta americana* nymphs. Parabiotic pair after the third postoperative molt, 73 days after fusion. *Note:* Eye on left partner has remained white.



The nonautonomous character of pigment development in the eye of the green mutant is also well illustrated by the transplantation of the two eye discs from the same green donor larva into two different larval hosts—one a green, and the other a wild-type host. Nine such paired transplantations were performed, but only four pairs in which both host partners survived were available for study. They showed that the eye discs in the green hosts always developed their own characteristic color—i.e., they remained yellowish green, while the partner discs in the wild hosts gave rise to eyes with wild-type pigmentation. Since the discs used came from the same donor larva, they were strictly comparable; this experiment is therefore an especially convincing demonstration of the dependency of the green eye for its color development on a diffusible factor in the wild-type host.

RELEASE OF DIFFUSIBLE SUBSTANCES FROM OTHER ORGAN TISSUES

The observation that the eyes of a green host can be made to develop color after the transplantation of a wild-type eye disc indicates that the substance responsible for this effect is released by the transplanted eye tissue. The question whether other tissues as well can bring about a similar effect was tested by implanting other organs or organ discs of wild-type larvae into green hosts. It was found that the eye color of green hosts remained unchanged after transplantation of antenna (7 cases), leg (8 cases), and haltere (1 case) discs. Testis transplants were also negative. However, the implantation of one wild ovary caused a slight color change in the eyes of two out of seven hosts tested. A very strong positive effect was produced after transplantation of Malpighian tubes (18 cases). One Malpighian tube changed the host eyes to red, while the implantation of two Malpighian tubes made them almost indistinguishable from wild-type eyes. An equally strong effect was obtained by transplanting Malpighian tubes from *Callitroga* larvae (4 cases) into green-eyed *Musca* mutants. The fact that ovary as well as Malpighian tube implants modify the eye color of the green host shows that the responsible substance is produced not only by the eye tissue but also by other parts of the body. The weak effects of the ovary transplants are perhaps not so difficult to understand if one recalls that one eye implant also often fails to change the host eye color. A single organ disc is apparently not sufficient to produce the amount of substance necessary for a clear color effect. Whether the ineffective organs, as for instance the leg discs, produce the diffusible principle below threshold or not at all is not known. As gaged by the strong eye-color effects, the Malpighian tubes

of *Musca* and *Callitroga* must release an appreciable quantity of substance. From evidence obtained on the Malpighian tubes of *Drosophila* (Beadle, 1937b), it appears that these structures not only produce but also store the effective substance. This may account for the strong effects observed in *Musca*.

TRANSPLANTATION OF EYE DISCS AMONG DIFFERENT GENERA

The next question to be discussed is whether the diffusible substance responsible for the color change of the green *Musca* eye toward wild type is also produced by other genera of Diptera. To this end a number of intergeneric eye grafts were performed. They are summarized in table 1.

First it must be pointed out that the transplanted eyes listed in table 1 differentiated to imaginal completion. The implants grown in green hosts developed their own characteristic wild-type pigmentation. Most important in this connection is the fact that the eye implants of four out of the five genera tested clearly caused a color change in the eyes of their green hosts. The diffusible principle responsible for this effect is thus produced by all these forms and operates effectively in intergeneric transplantations; it is therefore not genus specific. This conclusion is confirmed by the observation mentioned above that *Callitroga* Malpighian tubes change the eye color of green-eyed *Musca*.

The amount of pigment produced in the host eyes varied somewhat within the different combinations, but tended to be greatest in the *Cynomya* and *Sarcophaga* grafts. In *Musca*, with *Cynomya* implants, one individual was listed as showing a "strong" effect, three a "medium," and three a "weak" effect. The eye-color effects in the *Musca* group bearing *Sarcophaga* grafts were recorded as: 6 individuals "strong," 2 "medium," and 6 "weak." The only implants that produced no effect on the eye color of their hosts were those of *Fucellia*. It should be explained that *Fucellia* larvae were the smallest used in these experiments. One will recall that even a single wild *Musca* eye disc, which is considerably larger than a *Fucellia* eye disc, is often unable to elicit a detectable color response. Therefore it seems reasonable to assume that because of their small size the *Fucellia* grafts were unable to produce a sufficient amount of diffusible substance. If this should be the wrong interpretation, one would have to postulate for *Fucellia* an eye pigment system quite different from that of the other genera. This seems very unlikely, especially since *Fucellia* is assumed to be more closely related to *Musca* than are the other genera. Moreover, the eye color of the green *Musca* can be changed by feeding the

larvae on a medium to which ground-up *Fucellia* adults were added (Snyder, F. M., personal communication). From all this there seems little doubt that *Fucellia* implants, like those of the other genera, release into the blood of their hosts a substance that is able to change the pigmentation of the green eye toward wild type.

The implanted *Callitroga* eyes release perhaps the smallest amount of the diffusible substance as judged by the host eye-color effects in this series. From the 15 available cases, only 4 showed a "medium" effect, while the other animals showed a "weak" effect or none at all. Yet the transplantation of a green eye disc into a *Callitroga* host

TABLE I.—Summary of intergeneric eye transplantations

Donor	Host	Total number of cases	Color of implant	Host eye			
				Number of cases	Color	Number of cases	Color
<i>Callitroga</i>	<i>Musca</i> green	15	wild	11	changed toward wild	4	green
<i>Sarcophaga</i>	<i>Musca</i> green	14	wild	13	changed toward wild	1	green
<i>Cynomya</i>	<i>Musca</i> green	7	wild	7	changed toward wild	—	—
<i>Phormia</i>	<i>Musca</i> green	8	wild	8	changed toward wild	—	—
<i>Fucellia</i>	<i>Musca</i> green	4	wild	4	green	—	—
<i>Musca</i> green	<i>Callitroga</i>	19	changed toward wild	19	wild	—	—

demonstrates that this host must actually contain an appreciable amount of the effective substance, for all the implants gave rise to eyes with almost wild-type pigmentation. This experiment illustrates that as far as host eye pigment intensity is concerned, not too much reliance should be placed on the results of the "one eye disc" transplantations.

An attempt was also made to transplant eye discs from green *Musca* into *Cynomya* larvae. This failed, because all the hosts died in the pupal stage. Transplantations of late larval *Drosophila virilis* and *Aedes aegypti* eye discs into green-eyed *Musca* larvae were also unsuccessful. Here the hosts withstood the operation, but the grafted tissues degenerated completely.

TRANSPLANTATION OF EYE DISCS BETWEEN PHORMIA AND MUSCA

So far, it has been impossible to use *Phormia* larvae as hosts for transplantation experiments because the operated animals always die a few days after the operation, in the pupal stage. But *Phormia* eye discs can be successfully transplanted into *Musca* larvae. In order to test whether the formation of eye pigment in the green-eyed *Phormia* mutant depends, like that in the green-eyed *Musca* mutant, on activating influences exerted by the wild-type hosts, the following experiment was performed. Eye discs from mature green *Phormia* larvae were transplanted into wild-type *Musca* hosts of the same age. Since the donor eye discs were rather large, which greatly complicates the operation, they were halved before transplantation; thus, actually one-half an eye disc was transplanted into each host. From 26 individuals comprising this series, only 10 flies emerged. The implant in each host developed to imaginal completion and gave rise to eyes which showed almost normal wild-type pigmentation. These results seem clear. They indicate that the same factors necessary for pigment formation in the green *Musca* eye are also involved in bringing about pigment formation in the eye of the green *Phormia* mutant—for the same host elicits the development of pigment in the green *Musca* as well as in the green *Phormia* eye. That this is not the real state of affairs will, however, become evident in the following experiment.

Eye discs from green *Phormia* larvae were transplanted into green *Musca* hosts of the same age. In this series, consisting of 13 cases, it was found that in all individuals both implant and host eye had become pigmented. The reddish color which developed in the host and transplanted eyes almost resembled that of a wild-type eye. Precisely the same results were obtained in the second experimental series of this kind which consisted of 15 larvae from which 11 individuals emerged. Now the color development of a green implant in a green host and the induction of pigment formation in the green host eyes by a green implant can only be explained by the assumption that there must be at least two different diffusible substances involved in this effect. The transplant apparently provides the diffusible factor necessary for the development of pigment in the host eye—and this, in turn, produces the factor necessary for pigment formation in the implant. The biosynthetic chain leading to pigment formation is apparently interrupted at different points in these two mutants.

THE INJECTION OF PURE PIGMENT PRECURSOR SUBSTANCES

The importance of tryptophane metabolites in the biosynthesis of the brown eye pigment in *Drosophila* suggested an investigation of

the effects of these intermediates in *Musca* and *Phormia*. Kynurenine, identified as one of the diffusible substances found in *Drosophila*, was tried first on *Musca*. In this group of experiments, each of 21 green-eyed *Musca* larvae received approximately 6 mm.³ of a saturated solution of DL kynurenine by injection. All these animals emerged and showed an eye color almost identical with that of a wild-type fly. The course of events was quite different when DL kynurenine was supplied to green *Phormia* larvae. Here, doses of 14 mm.³ of a 65 percent saturated solution (3 cases), or 12 mm.³ of a saturated solution (7 cases) of DL kynurenine, completely failed to exert any effect on the eye color of these flies.

The next tryptophane metabolite tested was 3-hydroxykynurenine. Seventeen green *Musca* larvae each received about 8 mm.³ of a saturated solution of this substance, and as expected, the emerged flies were found to possess well-pigmented red eyes. The eye color of the green *Phormia* mutant was also changed to almost wild-type coloration by injection of 16 mm.³ of a saturated 3-hydroxykynurenine solution. From 25 injected individuals comprising this series, 21 emerged, all of which showed this strong eye-color effect. Thus, the formation of brown eye pigment can only be accomplished by the green-eyed *Phormia* mutant if the developing system is provided with 3-hydroxykynurenine, for kynurenine, which changes the eye color of the green-eyed *Musca* mutant, has no effect on the *Phormia* mutant. Evidently the *Phormia* mutant is unable to transform kynurenine into 3-hydroxykynurenine, that is, to bring about a biosynthetic step which the *Musca* mutant is able to perform.

EXPERIMENTAL ANALYSIS OF TESTIS PIGMENTATION

Under this heading are recorded some facts that were observed rather late in the course of the experiments; therefore, they are based on rather few cases. Taken in concert, the results of the various experimental series are uniform and the conclusions drawn from them are undoubtedly reliable.

The imaginal testes of *Musca*, as well as those of the other wild-type fly genera tested, possess a brownish pigment. The latter, contained in special pigment cells, covers not only the entire testis but also extends for a short distance along the vas deferens. The imaginal testes and vasa deferentia of the green *Musca* mutant are colorless. Now it was found that the brown testis pigment, like that of the eye, depended for its formation on the presence of a diffusible substance. For instance, the transplantation of a wild *Musca* eye disc into the

abdominal cavity of a green mutant host brought about pigment differentiation, not only in the host eye but also in the host testes. As a matter of fact, the diffusible substance necessary for eye pigmentation seems to be the same as that for testis pigmentation, because the various organ grafts that produce the diffusible substance and thereby elicit pigment formation in the host eyes were also effective in causing the formation of pigment in the testes. The evidence suggests that both eyes and testes of the green-eyed *Musca* mutant depend on the tryptophane metabolite kynurenine for completing successfully the biosynthesis of the brown pigment. One will notice from table 2 that there is an important difference between the eye and the testis as far as color development is concerned. The cells of a wild *Musca* eye disc are able to synthesize kynurenine or a kynurenine-like substance; an eye disc, therefore, always develops its brown color autonomously if grown in a green mutant host. This is not the case with the testis. A wild-type testis transplanted into a green mutant host remains colorless. The color development of a wild-type testis is a nonautonomous process, for it depends on a precursor substance produced by other wild-type tissues. In this respect, mutant and wild-type testes are alike.

EXPERIMENTS ON PERIPLANETA AMERICANA

Studies on the biosynthesis of the tryptophane-derived brown eye pigment, using eye-color mutants as a tool for the analysis of pigment formation, have so far been conducted only on holometabolous insects. The major and final steps leading to the actual synthesis of pigment in the pigment-carrying eye cells take place in these forms during the differentiation of the imaginal eye in the pupal stage. In hemimetabolous insects, which already in their nymphal stages possess a fully differentiated compound eye, the course of events must be different. The formation of eye pigment must have occurred here during embryonic development. Therefore, it might seem useless to attempt the induction of pigment formation in the nymphal eyes of these creatures, because the metabolic events responsible for eye pigmentation must have already run their course at this stage. But this is not the case.

The nymphal eye grows from instar to instar by the addition of new facets from a so-called budding zone. In this zone, during the intermolt periods, the formation of new imaginal eye elements occurs, much the same as it does in the eye disc of a fly during pupal life. The budding zone must be considered the prospective eye anlage for the

imaginal eye of the hemimetabolous insect, just as the eye disc is the prospective anlage for the imaginal eye of the holometabolous insect. Thus it should be theoretically feasible to detect the presence of diffusible eye pigment precursors by the color reaction in the newly formed facets of the eye, provided an eye-color mutant lacking the brown eye pigment is available. We are fortunate to have in our *Periplaneta americana* cultures a mutant stock with white-yellow eyes. The normal eye color of the American roach is a dark brown. Is the lack of pigment in the eyes of the mutant roach caused by a genetic block that prevents the formation of a diffusible intermediate metabolite necessary for pigment differentiation? To test this, one should transplant, as was done in Diptera, the nymphal eye, including the

TABLE 2.—*The influence of various implants on the testis color*

Type of donor	Kind of tissue transplanted	Host	Number of cases	Effect on testis color
<i>Musca</i>	eye	<i>Musca</i> green	2	positive
<i>Musca</i>	Malpighian tubes	<i>Musca</i> green	1	positive
<i>Musca</i>	ovary	<i>Musca</i> green	3	positive
<i>Musca</i>	testis	<i>Musca</i> green	2	negative
<i>Phormia</i>	eye	<i>Musca</i> green	3	positive
<i>Phormia</i> green	eye	<i>Musca</i> green	4	positive
<i>Sarcophaga</i>	eye	<i>Musca</i> green	3	positive
<i>Callitroga</i>	eye	<i>Musca</i> green	4	positive
<i>Callitroga</i>	Malpighian tubes	<i>Musca</i> green	3	positive
	DL. kynurenine	<i>Musca</i> green	9	positive

budding zone, from a white-eyed roach into the body cavity of a normal wild-type roach. But technical difficulties preclude this method of approach. However, it is possible to unite in parabiotic fusion two nymphal roaches (Bodenstein, 1953). The fused partners soon grow together, molt in synchrony after an appropriate interval and in exceptional cases are able to molt several more times. The blood circulates freely from one partner to the other in such a parabiotic pair. Therefore, any pigment precursor present in the blood of the normal partner can pass into the mutant partner and will be able to exert its effect here. The principle of this method is the same as that of transplantation, for both are designed to allow diffusible substances in the blood of the animal to come into contact with the developing eye tissues.

With this information as a background, the experiments performed on *Periplaneta* can be discussed. They consist of five parabiotic pairs. In each, a 9th-stage normal nymph was combined in parabiosis with a younger (5th to 6th stage) nymph of the mutant white-eyed stock.

Two of these pairs died about 14 days after the operation, at which time no change was observed in the eye color of the white partner. The 3d and 4th pairs molted 28 and 31 days respectively after the operation. The molted white partners in both of these pairs also showed no eye color effects. The 5th pair molted for the first time 28 days, for the second time 50 days, and for the third time 73 days after the operation. The normal partner of this pair was after its 3d molt still in the nymphal stage, showing that under the influence of the young mutant partner, it had undergone a supernumerary nymphal molt—for *Periplaneta* normally has 10 nymphal stages (Bodenstein, 1953). The eye color of the white partner was as in the other cases not affected, although this animal remained for 73 days in blood connection with its normal wild-eyed partner (pl. 1). These results leave no doubt that the white eye of the *Periplaneta* mutant develops autonomously as far as its color is concerned, and that it is unable to respond with pigment formation to diffusible pigment precursors that circulate in the blood of the wild-type roach.

The actual presence of diffusible tryptophane metabolites in the roach was demonstrated in the following series of experiments. (1) Forty-five 6th- to 7th-stage wild-type roach nymphs were killed by boiling and then ground up in a Waring blender in 50 cc. of the food medium used for our *Musca* cultures. This medium was divided between two culture bottles, each containing 25 cc. of the mixture. Seventy-five 1st-instar larvae of the green *Musca* mutant were placed in each bottle and allowed to grow to maturity. (2) The same experimental procedure was repeated, but instead of 45 roach nymphs, 105 individuals were ground up in 50 cc. of the culture medium. (3) As a control, the same number and type of larvae were grown in 25 cc. of culture medium, to which no roach material was added. This normal medium consists of 5 g. powdered milk, 5 g. brewer's yeast, 0.75 g. agar, 0.15 g. Tegosept in 50 cc. H₂O. The eye color of the 118 flies that emerged from the control series was unchanged. Every individual showed the typical greenish-yellow eye coloration characteristic for this *Musca* mutant. A slight but definite change in the eye color toward pink was observed in most of the 132 flies that emerged from the first experimental series. The intensity of the color change varied somewhat between the different individuals, ranging from a slightly off-color to a distinct but light pink. The eye-color effects were much more pronounced in the 87 flies that emerged from the second experiment. Here the eyes of every fly were affected, although again the intensity of the effect varied within the different individuals. The

majority of these flies had slightly pink eyes, but several showed a clear reddish tinge.

The evidence provided by the above experiments suggests that the nymphs of *Periplaneta americana* (wild) contain in their internal environment tryptophane-derived diffusible pigment precursors that can be utilized by the green *Musca* mutant for the formation of eye pigment. Since the eye-color development of this mutant is kynurenine dependent, it follows that *Periplaneta* contains in its system a kynurenine-like substance.

DISCUSSION

THE CASE FOR MUSCA

Several pertinent facts concerning the eye-color development in Diptera are revealed by the experimental results presented. In the green *Musca* mutant, kynurenine is a substitute for a wild-type eye implant. This implies that the effective diffusible substance released by the wild-type eye disc is kynurenine or a kynurenine-like compound. This mutant is apparently unable to synthesize kynurenine from a precursor substance and thus the eye remains colorless. However, the mutant animal contains in its metabolic makeup the prerequisites necessary to complete pigment synthesis after the system is provided with kynurenine. The situation encountered here much resembles that found, for instance, in the *Drosophila* mutant vermilion (*v*) and in the *Ephesia* eye-color mutant *a*. In both these mutants, the transformation of tryptophane into kynurenine is blocked and the mutants accumulate tryptophane. Corroborating evidence that the green-eyed *Musca* mutant is also unable to convert tryptophane into kynurenine, has been supplied recently by Ward and Hammen (1957), who found that this mutant accumulates tryptophane. Pigment synthesis is blocked at a different point in the metabolic chain in the green *Phormia* mutant, for injection of kynurenine into the system of this fly has no effect on the eye color. Since 3-hydroxykynurenine injection is effective, it is indicated that the metabolic block lies beyond kynurenine. This state of affairs has its parallel in other insects. It was first observed in the *Drosophila* mutant cinnabar. To complete the biosynthesis of the brown eye pigment this animal, like our *Phormia* mutant, needs the so-called cinnabar substance (*ca*) which was later identified as 3-hydroxykynurenine. Thus, the lack of the brown eye pigment in the two dipteran mutants investigated is caused by the inability of the mutant systems to transform tryptophane-derived pigment precursors either into kynurenine (*Musca*) or into

3-hydroxykynurenine (*Phormia*). Because of these results it is obvious that the biochemical system underlying the expression of the brown eye pigment in both these Diptera is very similar to that observed in other insects.

It may be recalled that the diffusible precursors necessary for the production of pigment in the mutant eye tissue of *Musca* are also effective in bringing about pigment formation in the colorless testes of these mutants. The principal biochemical events leading to pigment synthesis are apparently the same in these two organs. There are other examples with like implications. In *Ephestia*, for instance, transplantation of testes from a wild-type donor into a mutant host lacking the brown pigment brings about pigment formation not only in the eye but also in the testis sheath, the ocellus, the imaginal brain, and in the larval hypoderm (Kühn, Caspari, Plagge, 1935). Similarly in the *Drosophila* vermilion brown, pigment formation can be induced in the colorless ocelli as well as in the eye by supplying the larva with V+ substance, i.e., with kynurenine (Beadle, 1937a). Various organs can produce the diffusible pigment precursors. Yet, a given organ of one species may release the diffusible principle, while the same organ belonging to another insect group may not. It was also found that certain tissues can synthesize both, and others only one, of the pigment precursor substances (Becker, 1938). As far as the tissues that produce the precursors in *Musca* are concerned, the situation encountered here much resembles that found by Beadle (1937a) for *Drosophila*. In both these forms, the eye discs and the Malpighian tubes produce kynurenine, i.e., V+ substance, while the testes do not. But unlike *Drosophila*, the ovaries in *Musca* seem to produce a limited amount of this substance. The nonspecificity of the pigment precursors as revealed by the intergeneric transplantations comes as no surprise. It has been known for a long time (Becker, 1938) that they are physiologically interchangeable among different species, genera, and even families.

THE CASE FOR PERIPLANETA

The presence of tryptophane-derived pigment precursors in nymphs and the inability of the *Periplaneta* white-eyed mutant to utilize these metabolites indicates that the mutant genes block the formation of other apparently not diffusible compounds necessary for pigment development. What they are, we do not know. However, it is of interest to note in this connection that a similar situation appears to exist in certain *Drosophila* (Ephrussi and Chavais, 1937) and Lepidoptera

mutants (Schwartz, 1940 and 1941; Kühn and Schwartz, 1942). It has been shown, for instance, that the white eye of the *Drosophila* mutant *w* remains colorless on transplantation into a wild-type host. Likewise, if the pupal eye of the white-eyed *Ephestia* mutant *wa* or that of the geometrid *Ptychopoda* mutant *dec* is transplanted into its respective wild-type host pupa, it can be shown that the color development of the mutant eye is autonomous. The reciprocal experiment, namely, the grafting of a wild-type pupal eye into the pupa of the mutant host, gives the same result. In all these combinations, there is no influence of the graft on the eye color of the host, nor one of the host on the eye color of the graft, although as other experiments had shown, the wild-type forms contain tryptophane-derived diffusible pigment precursors in their blood. Now, in the *Ephestia* mutant *a* the formation of the brown eye pigment is kynurenine dependent. The eye color of this animal can therefore be changed toward wild type by the transplantation of a wild-type eye, because the graft produces the pigment precursor kynurenine (*a*+substance) which is needed for pigment formation in this mutant. Beyond this, it has been demonstrated that when part of a pupal eye from an *Ephestia* mutant *wa* or a *Ptychopoda* mutant *dec* is transplanted into the pupal eye region of an *Ephestia* mutant *a*, the host eye pigmentation changes toward wild type, while the grafted pieces develop the pigment characteristics of their own genotypes. The implication of these results is clear. The eye tissues of the *wa* and *dec* mutants release the pigment precursor *a*+substance (kynurenine), although they cannot use this metabolite for the formation of their own pigment. A similar situation has been described for *Drosophila*, in the mutant of the *w* series (Ephrussi and Chavais, 1937).

To return to *Periplaneta*: The white-eyed *Periplaneta* mutant, as shown by the studies of Ward and Hammen (1957), seems to accumulate tryptophane. Evidently, in *Periplaneta* as in the green *Musca* mutant, a genetic block prevents the transformation of tryptophane into kynurenine. Yet the white-eyed *Periplaneta* mutant does not change its eye color when in parabiotic fusion with a wild-type partner, although as revealed by the feeding experiments, kynurenine is present in the blood of the wild-type partner. Apparently, the white *Periplaneta* eye is unable to utilize the kynurenine supplied by the wild partner. But this suggests the presence of a genetic block at still another point in the biosynthetic chain in the white *Periplaneta* mutant.

Now, it is known that the final pigment granules are bound to proteinaceous carrier granules in the cytoplasm of the cell. As a matter

of fact, the last steps of the progress of pigment synthesis seem to be possible only in close association with these protein particles onto which the pigment is deposited. In the absence of these carrier granules, pigment fails to develop (Hanser, 1948; Caspari, 1955). This occurs, for instance, in the *Ephestia* mutant *wa*. Although the tryptophane-derived diffusible pigment precursors are formed by this mutant, its eyes remain colorless because the *wa* gene in some manner interferes with the development of the carrier granules. Therefore, the introduction of even large amounts of diffusible tryptophane metabolites into the system of these animals has no effect on the eye color. In the light of these considerations, it seems possible that a similar mechanism prevails in the white-eyed *Periplaneta* mutant; for, as the parabiosis experiments have shown, the white-eyed partner does not change its eye color when subjected to the tryptophane metabolites that circulate in the blood of the wild-type partner. Proof for this contention has, however, to await further investigation.

SUMMARY

The biosynthesis of the brown eye pigment in two dipteran eye-color mutants, one in *Musca domestica* and the other in *Phormia regina*, has been investigated by transplantation and injection experiments. The eye color of these two mutants is a yellowish green, strikingly different from the reddish-brown eye of the wild-type flies.

1. When the larval eye disc from a wild *Musca* donor is transplanted into the larva of a green *Musca* host, the transplant gives rise to an imaginal eye of wild-type pigmentation. Moreover, the grafted eye changes the green eye color of the host eyes toward pink. The wild-type transplant, therefore, must have released into the blood of the host a diffusible substance necessary for the formation of pigment in the green eye. The dependence of the mutant eye for pigment development on a substance released by the wild-eye tissue is clearly demonstrated by the transplantation of a mutant eye disc (green) into wild-type host larvae. In this combination it is found that the green-eyed implant gives rise to a pigmented imaginal eye almost indistinguishable in color from a wild-type eye.

2. The diffusible principle responsible for these eye-color effects is also released by tissues other than the eye of the wild-type fly. Transplanted ovaries and Malpighian tubes cause a color change in the eyes of the green host, while antenna, leg, or haltere discs as well as testis transplants have no effect.

3. The diffusible principle is also not genus specific, for eye discs

of wild-type *Callitroga*, *Sarcophaga*, *Cynomya*, and *Phormia* larvae transplanted into mutant *Musca* larvae change the green host eye color toward wild-type coloration. The transplantation of *Callitroga* Malpighian tubes into the mutant host has the same effect.

4. Eye discs from the green *Phormia* eye mutant transplanted into wild-type *Musca* hosts develop to imaginal completion and give rise to eyes with almost normal wild-type pigmentation. Therefore, the *Musca* host must contain, in its organic environment, a diffusible factor needed by the green *Phormia* eye for pigment development. Although pigment formation is elicited in the green *Musca* as well as in the green *Phormia* eyes by the same host, the factors responsible for these happenings are not the same, because when eye discs of green *Phormia* larvae are transplanted into green *Musca* larval hosts, both transplant and host eyes become pigmented. This result can only be explained by the assumption that at least two different diffusible substances are involved in this effect.

5. Injection of pure tryptophane-derived pigment precursor substances into both mutant types has clarified the issue further. It was found that injection of kynurenine into the green-eyed *Musca* mutant changed the eye color of this host toward wild, while injection of this compound into the green-eyed *Phormia* mutant had no effect on the eye color of these flies. On the other hand, injection of the metabolite 3-hydroxykynurenine gave positive results, i.e., it changed the eye color of both the *Musca* and the *Phormia* mutant toward wild type. The biosynthetic chain leading to pigment formation is apparently interrupted at different points in these two mutants. The *Musca* mutant is unable to convert tryptophane into kynurenine, while the *Phormia* mutant cannot transform kynurenine into 3-hydroxykynurenine.

6. The sheath of the imaginal testis in *Musca* contains cells with brownish pigment, while the testis of the green-eyed *Musca* mutant is colorless. The experimental evidence shows that both eye and testis of the green-eyed *Musca* mutant depend on the tryptophane metabolite kynurenine for completing successfully the biosynthesis of the brown pigment. Yet the testis of the wild-type *Musca*, in contrast to its eye, is unable by itself to synthesize kynurenine and therefore depends for its normal brown coloration on the production of this substance by other wild-type tissues.

7. The question whether pigment formation is elicited by diffusible substances circulating in the blood has also been investigated in an eye-color mutant of the American roach *Pcriplaneta americana*. This mutant has white-yellowish eyes, while the normal roach eye is a dark

brown. Experiments were performed in which a white-eyed mutant was combined in parabiotic fusion with a normal animal. It was found that although such pairs lived for several weeks and had established perfect blood connections, the eye color of the mutant individual was not affected by the normal partner. The white *Periplaneta* eye is apparently unable to utilize tryptophane-derived diffusible pigment precursors which circulate in the blood of normal *Periplaneta*.

8. In the discussion, the results of these studies are compared and related to findings of other investigations. These efforts reveal that the biosynthesis of the brown eye pigment in *Musca*, *Phormia*, and *Periplaneta* is in general similar to that found in other insects.

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THE STRUCTURE AND SOME ASPECTS OF DEVELOPMENT OF THE ONYCHOPHORAN HEAD

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The position of *Peripatus* relative to the arthropods on the one hand and to the annelids on the other has led to an amount of attention paid to this animal all out of proportion to its inoffensive, retiring, and unspectacular habits. The reasons for this attention are not difficult to understand when one considers that it apparently represents a link between two very important phyla.

The characters wherein *Peripatus* appears to be close to the arthropods are striking and significant. The body wall is similar to that of many arthropods. The appendages diverge from the chaetal type found in the annelids and exhibit more the embryological and later developmental growth found in the arthropods. In fact, Snodgrass (1938) considers the walking leg of *Peripatus* to be the prototype of the arthropod limb.

Peripatus has on the other hand definite relationships with the annelids. It is wormlike with no distinct body regions. In the adult stage it has no definitely segmented areas, though it has a head region distinct in function from the rest of the body. Internally the nerve cord is distinctly similar to the annelid type, though the anterior end, especially the brain, shows some advances in structure.

Internally, the alimentary canal, especially in the anterior end and the middle sections, and the peritrophic membrane, especially in its origin, are strikingly similar to those of the insects. The heart also exhibits the more simplified form found in insects and in some other arthropods. Is it any wonder, then, that over the long period of years during which workers have investigated this animal many of them have considered it to belong to the phylum Arthropoda?

I do not wish, within the limits of this paper, to make an extended study of the literature on *Peripatus*. That has been thoroughly done by several others, and those who wish to pursue that subject further I refer to the bibliographies in the works of Snodgrass, Manton, and Weber.

Any work in connection with the head of an invertebrate such as *Peripatus* inevitably must include a discussion of segmentation. Of the many workers who have applied themselves to this problem there are several who in late years have either contributed original data as a result of their own research or have written compilations that are extremely valuable to the anatomist. Of these workers, Federov (1929) alone of the group confined himself to a single organ system of the adult in his two extensive papers on the nervous system of *Peripatus tholloni*. Realizing the importance of the nervous system as a criterion of segmentation, he tried to identify segmental areas in the ventral nerve chain of the animal and to correlate the cerebral nerves with the nerves of these segmental areas.

Pflugfelder (1948) in a paper on the embryology of *Paraperipatus amboinensis* comes to conclusions concerning head segmentation that support Federov's ideas. Pflugfelder, however, was handicapped by the fact that he apparently considered the jaws of *Peripatus* to correspond to the mandibles of the arthropods, and he formulated his arguments to prove this point, a fact which I think limits the value of his work.

Manton in a series of papers published after 1938 has given very valuable accounts of the embryology, anatomy, and habits of *Peripatus*. But her work on embryology was mainly concerned with the thesis that segmentation is instigated by the mesoderm and that in this respect the nervous system is of little importance. More will be said about the work of these two later in this paper.

Snodgrass, in his paper of 1938 on the Annelida, Onychophora, and Arthropoda, gave a remarkably clear and complete description of the development and anatomy of this animal.

Weber, in his "Morphologie, Histologie und Entwicklungsgeschichte der Articulaten" published in 1952, devoted a lengthy section to the Onychophora in which he compared the ideas of L. M. Henry (1948) to those of Pflugfelder published the same year. He agrees with Pflugfelder's opinion that the jaws of the Onychophora are the true mandibles as opposed to Henry's statement that they belong to the tritocerebral segment. In his paper Weber quotes Pflugfelder at length in regard to principles to be followed in homologizing organs in different groups of animals. He says, "Care must be taken not to homologize in all details the tritocerebrum of the Onychophora and the stomatogastric nerves emanating therefrom with the tritocerebrum of the Arthropoda on the one hand and the corresponding parts of the nervous system of Annelida on the other. The Onychophora do not

represent a conglomerate of characteristics of Arthropoda and Annelida but despite the apparent mixture of characteristics of both animal groups, they represent harmonious animals in which individual differences are present."

Pflugfelder makes this statement after discussing the relationship of the first postoral commissure to the "jaws" or, as he considers them, the "mandibles." I agree that one should be careful in forming homologies, but the same principles apply to the mandibles themselves, and in regard to these very important organs Pflugfelder is so convinced that the onychophoran "jaws" are true mandibles, that he interpolates what I consider to be an entirely imaginary ventral organ and ganglion between the mandibles and the antennae in order to provide a "premandibular" segment in the Onychophora that will be homologous with the premandibular segment of the arthropods.

My purpose in undertaking this research problem was to make a thorough anatomical study of the head region and particularly the "jaws" and then to review the embryonic development of the head to see if a different interpretation would be justified. The form used for the dissections in this study was *Peripatoides novae-zealandiae* (Hutton).

The head of *Peripatus* (fig. 1 A) is an undifferentiated region of the body, unmarked by sutures or grooves that would give any clues as to its limits or segmental areas. The antennae (*Ant*) are large and are situated on the extreme anterior end on the dorsal side. Beneath them and slightly caudad are the inconspicuous eyes and the opening into the preoral cavity (*Pcav*). This cavity is ringed with lobes that form lips which when pressed together effectively close the mouth. Deeply enclosed within the preoral cavity are the feeding claws (*Fcl*), with only their tips exposed in the preoral opening. The first pair of appendages behind the mouth are the slime papillae (*Slp*) called by some investigators the oral papillae, and behind them are the first pair of legs.

A series of parasagittal dissections will indicate the limits of the preoral cavity and its relation to the real mouth opening which lies within the cavity itself (fig. 2 A, B, C, D). In preparation for A, the head surface was removed on the dorsal side, revealing the brain (*Br*) and the circumoral folds (*Cof*). In this figure the two teeth of the right feeding claw (*Fcl*) are prominent.

The walls of the preoral cavity are deeply folded in such a way that the lobes (*Di*) formed between these folds are arranged radially and extend onto the outer surface of the body (figs. 1 A, 2 A).

In the dorsal wall of the preoral cavity there is located an enlarged lobe called by Snodgrass the "labral lobe" but by Manton and others the "tongue" (figs. 1 A, 2 A, *Dl*). Though this structure appears to be independent of the ring of lobes around the edge of the opening, I believe that it is simply one of the circumoral lobes greatly enlarged

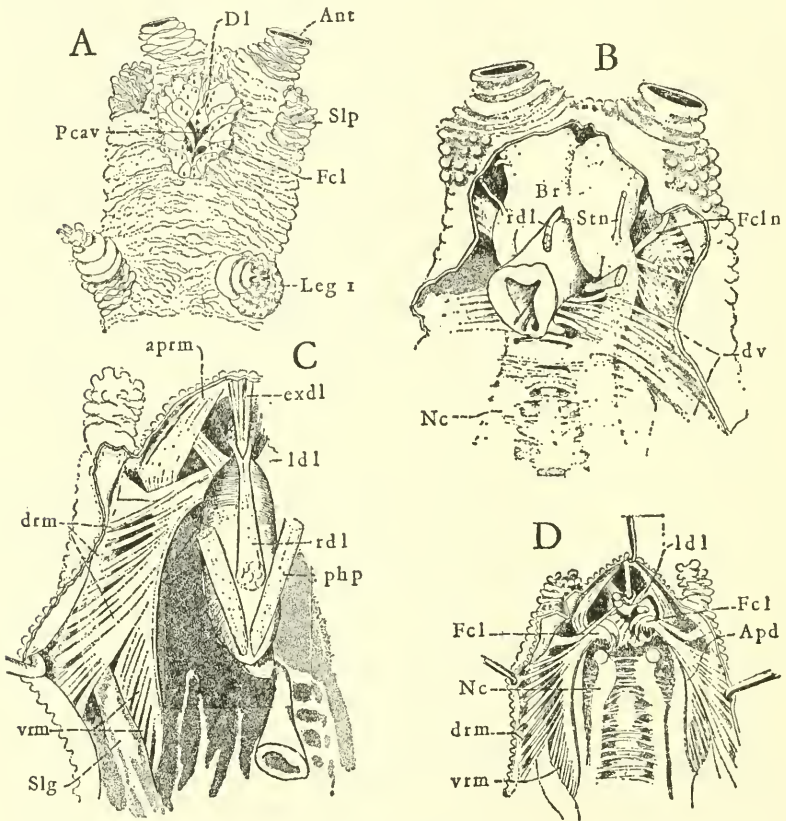


FIG. 1.—Onychophora. Internal structure of the head of *Peripatoides novae-zelandiae*.

A, head from ventral side. B, dorsal dissection of head showing brain and associated structures. C, same with brain removed. D, same with brain and oesophagus removed.

Ant, antenna; *Apd*, apodeme of feeding claws; *Fcl*, feeding claws; *Fcln*, feeding claw nerve; *Dl*, dorsal lobe; *Br*, brain; *Nc*, ventral nerve cord; *Pcav*, preoral cavity; *Slp*, slime or oral papillae; *Slg*, slime gland; *aprm*, anterior protractor muscles of the feeding claws; *drm*, dorsal retractors of the feeding claws; *dv*, dorsoventral muscles; *exdl*, anterior extensor muscles of the dorsal lobe; *ldl*, lateral dilators of dorsal lobe; *php*, protractor muscles of pharynx; *rdl*, retractor muscle of dorsal lobe; *vrm*, ventral retractors of feeding claws.

to form an organ to help in the swallowing of food. Though it is equipped with powerful muscles and has a row of external spines, in these respects resembling somewhat the epipharynx of some insects, it cannot in any way be considered as a labrum. Neither is it a tongue in the sense that the hypopharynx of chewing insects is a tongue. It simply is one of the circumoral ring of lobes, though much larger than

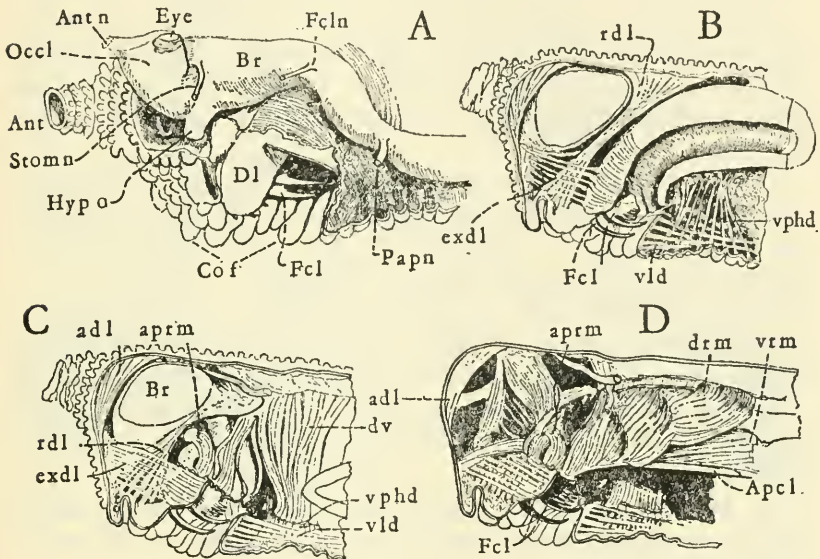


FIG. 2.—Lateral dissections of the head.

A, vertical dissection with brain in place, dorsal body wall removed. B, median dissection with brain cut. C, same with oesophagus removed. D, same with brain removed.

Antn, antennal nerve; *Apcl*, apodeme of feeding claws; *Br*, brain; *Cof*, circumoral folds; *Fcl*, feeding claws; *Fcln*, nerve of feeding claw; *Hypo*, Hypocerebral organs; *Occl*, ocular lobe; *Papn*, papillar nerve; *adl*, anterior dilators of the oral lobes; *aprm*, anterior protractors of the feeding claws; *exdl*, anterior extensors of the dorsal lobe; *drm*, dorsal retractors of the feeding claws; *dv*, dorsoventral muscles; *vld*, ventral longitudinal dilators of the oral lobes; *vphd*, ventral dilators of the oesophagus; *vrm*, ventral retractors of the feeding claws.

any others in the preoral cavity, and is here called the dorsal lobe (*Dl*).

Now let us examine this structure more closely. When the mouth is closed it is apparent that this dorsal lobe closes the opening by fitting tightly within the circle of other lobes. When the animal relaxes the muscles of the mouth region, the mouth opens wide and the dorsal lobe may be pushed out and retracted. The spines on its lower keel-

like edge, though small, are slanted backward, and it is apparent that they aid in pushing food back into the oesophagus.

A dorsal dissection indicates that there are two sets of muscles concerned with the movement of this lobe (fig. 1 C). They are:

1. The anterior extensor of the dorsal lobe; a bundle of several fibers arising on the anterior head wall and inserted on the wall of the oesophagus where the lobe joins the oesophagus (fig. 1 C, D, *exdl*).

2. The median retractor of the dorsal lobe; a large muscle bundle attached to the dorsal body wall, extending forward where it forks to pass around the anterior extensors of the dorsal lobe, each branch being inserted on the posterior median wall of the dorsal lobe (fig. 1 C, *rdl*).

Laterad of the retractor of the dorsal lobe there are two diagonal muscles which, though not attached directly to the base of the lobe, are closely associated with muscles 1 and 2 and have considerable effect on the functioning of the lobe. They are:

3. The lateral dilators of the pharynx originating on the body wall, passing inward underneath the anterior protractors of the feeding claws (*aprm*) to their insertions on either side of the oesophagus. These muscles resist the pull of the median retractors and are in turn opposed by the action of the circular muscles of the oesophagus (fig. 1 C, D, *ldl*).

On the anterior surface of the head there is a group of muscles directly concerned with the opening and closing of the preoral cavity. These muscles are:

4. The anterior dilators of the preoral lobes; muscle fibers arising dorsad on the front of the head; inserted at the base of the lobes at each side of the median dorsal lobe (fig. 2, B, C, D, *adl*).

Other muscles concerned with the swallowing of food, though they are not actually attached to the oral lobes, are the following:

5. The ventral pharyngeal dilators. These are vertical muscles consisting of distinct fiber bundles originating on the ventral median body wall and inserted dorsally on the underside of the oesophagus (fig. 2 B, C, D, *vphd*).

Several groups of muscles in the head consist of flattened fibers lying in sheets close to the body wall. These sheets are very thin and appear almost membranous. These are:

6. Ventral longitudinal dilators of the oral lobes. These are divided into two bands originating on the ventral body wall, extending forward, one band on each side of the ventral pharyngeal dilators and inserted in the walls of the ventral posterior oral lobes (fig. 2 B, C, D, fig. 3 A, *vld*).

7. Lateral dilators of the oral lobes; large flat sheets of muscles originating on the body wall near the bases of the antennae; inserted in the large lobes adjoining the median dorsal lobe (fig. 3 A, *ldm*).

8. Lateral sphincter muscles of the oral lobes. These are large sheets originating on the anterior head wall; inserted ventrally and

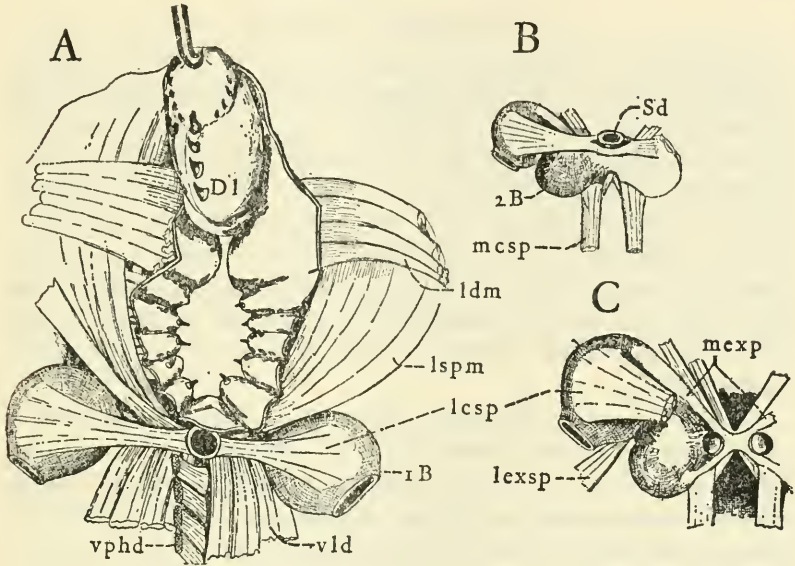


FIG. 3.—Dissections of the oral lobes, and the salivary pump.

A, dorsal dissection with inner wall of preoral cavity removed showing salivary pump. B, salivary pump with ventral muscle sheet removed to expose the entire salivary pump. C, same dissection with the median salivary duct removed.

lB, outer lobe of salivary pump; *2B*, inner lobe of salivary pump; *Dl*, dorsal lobe; *Sd*, salivary duct; *lcsp*, lateral compressors of salivary pump; *ldm*, lateral dilators of the oral lobes; *lexsp*, lateral extensors of the salivary pump; *lspm*, lateral sphincter of the oral lobes; *mcsp*, median compressors of salivary pump; *mexp*, median extensors of salivary pump; *vld*, ventral longitudinal dilators of the oral lobes; *vphd*, ventral dilators of the oesophagus.

posteriorly in the oral lobes near the insertions of the ventral longitudinal dilators of the oral lobes (fig. 3 A, *lspm*).

These muscles lie exterior to the lateral dilators of the dorsal lobes and, when contracted, pull the ventral oral lobes together, thus helping to close the mouth.

Other small sheets of muscles not shown in the figures for this paper lie near the body wall and are inserted in the lobes, apparently just a few fibers to each lobe. Some of these lie underneath the lateral sphincter muscles and are inserted in the lateral oral lobes much as

are the lateral dilator muscles. Others lie beneath the ventral longitudinal dilators and function in a similar fashion to those muscles. Since these small sheets of muscles have the same apparent function as the larger muscles with similar insertions that are adjacent to them, they are not assigned separate numbers in this list.

THE SALIVARY GLANDS

A dissection in which the alimentary canal is removed and the mouth and preoral cavity are arranged so that one, in examining the preparation, looks out the mouth opening (fig. 3 A), reveals not only the musculature of the oral lobes very clearly, but also indicates that the salivary ducts are formed into a series of complicated folds that form very effective valves. Each salivary gland empties into a button-shaped chamber (*IB*) lying laterad of the ventral longitudinal sheet of muscles (*vld*). The common salivary duct (*Sd*) lying between these chambers is connected to each chamber by narrow bands of muscles, each band fanning out distally where it inserts on the chamber (*lcsp*).

When the ventral longitudinal sheets of muscles are removed, a second swelling in each lateral duct is revealed lying mesad and slightly underneath the first chamber (figs. 3 B, C, 2 B). These chambers form not only an effective salivary pump but also the valves that are so necessary in the operation of such a pump.

The muscles that operate the pump and valves are as follows:

9. The paired lateral compressors of the salivary pump originating on the walls of the median salivary duct; inserted on the outer chamber (fig. 3 A, B, *lcsp*). These muscles by their contraction close the valve between the pump and the salivary gland when the salivary juice is being ejected from the common duct into the preoral cavity.

10. The median compressors of the salivary pump. A pair of longitudinal muscles lying near the center line originating on the body wall and inserted on the inner edge of the inner chamber of the pump (fig. 3 B, C, *mcs*). These muscles when contracted prevent a twisting movement of the lateral ducts, thus aiding in the closing of the passage between the two chambers.

The compressor muscles are opposed in their action by several small muscles that, when they contract, together open the passage between the two chambers. They are:

11. The lateral extensors of the salivary pump. Each muscle of this pair is attached distally to the body wall and medially to the inner edge of the outer chamber (fig. 3 C, *lexsp*).

12. The median extensors of the salivary pump. A group of small muscles that are intimately associated with the small muscles under 6 (*vld*). They appear to form an X underneath the common duct where they attach to the body wall. Distally they insert along the edges of the inner chamber, one anterior to the duct, the other posterior to the duct on each side (fig. 3 C, *mexp*).

The action of these muscles together with the lateral extensors apparently straightens out the two chambers on each side, thus opening up the passage between them; in other words, they open the valve.

Many other small fibers already assigned to muscle *vld* converge on the center line at the same point. Others of this group lie on top of the inner chambers and appear by their action to compress the inner chambers. I did not find any other valve mechanism that would prevent liquid from reentering the ducts when the compressor muscles are relaxed. It may be that the action of the longitudinal muscles just mentioned would accomplish this purpose by forcing the median chambers closed when the lateral chambers are extended by the relaxation of muscles 11 and 12.

THE FEEDING CLAWS

The "jaws" of *Peripatus* consist each of a pair of long, slender claws (figs. 1 D, *Fcl*) protruding into the oral cavity from their bases which are deeply invaginated within the body (figs. 1 A, 2 A, B). Only their tips are to be seen lying across the mouth opening. From their inner ends long apodemes (*Apd*) extend into the body cavity, and to these, powerful muscles are attached. The muscles are capable of acting as protractors or retractors, the retractor muscles also acting as flexors of the claws. These organs have been the subject of a great deal of investigation, and many views have been presented as to their segmental relationships. Some German workers apparently have been convinced not only that they are true jaws but that they are homologous with the mandibles of the arthropods. However, though they lie almost in the same plane, they are not opposed to each other and in fact do not in the least act as true jaws. They are not crushers or chewers of food but they act instead as claws or rakes with which the animal simply scratches particles of food away from the food source so that other mechanisms of the ingestive apparatus are able to move them into the mouth in a position to be swallowed.

Further comparison with the arthropod mandible reveals pertinent facts which may give us a clue in identifying the segment to which

they belong. In the arthropods, though the appendages constituting the mouth parts of chewing forms are considered to be modified legs, the actual working structures of the mandibles, maxillae, and the labium where one is present, are formed from endite lobes of the two basal segments of the telopodite according to Snodgrass (1935). The telopodite becomes reduced and acts as a sensory organ or, in the case of the mandibles, is lost entirely.

Though appendages of both the Onychophora and the Arthropoda have had a common origin as lobiform outgrowths of the body wall, nothing like the elaborate development of the leg of arthropods takes place in the Onychophora. The differentiation of the onychophoran leg into a thick basal part and a slender distal part, as Snodgrass says (1938), might be seen as an incipient segmentation, but the development of endite lobes on the basal leg segments of arthropods into the chewing and crushing structures we call mandibles finds no parallel development in the Onychophora.

The "jaws" of *Peripatus* are simply the claws at the end of the appendage, greatly enlarged when compared with the claws of the walking legs but not greatly different from them in function. Tiegs (1949) recognized this when he said that the "jaws" of *Peripatus* were merely enlarged claws. Also they are not retracted simultaneously as are the mandibles of a chewing insect for example, but are retracted alternately, according to Manton (1937). For these reasons the term "jaws," though firmly established in the literature, is incorrect, and the organs should be designated as the "feeding claws."

To understand how these claws work one must consider them as the tip ends of greatly strengthened legs which have been withdrawn into the body so that just the tips of the claws project into the oral cavity (figs. 1 A, 2 A, B, C, D). The muscles then taking them from the anterior to the posterior consist of the following groups:

13. Anterior protractor of the claws (fig. 1 C, D, *aprm*), a powerful group of muscles arising anteriorly on the head wall and inserted at the base of the claws. (The apparent distortion of these muscles indicated in the sketch is probably due to stresses put upon them by the hooks holding the dissection in place.)

14. The dorsal retractor of the claws (*drm*) consisting of widely spaced fibers originating on the body wall above the slime gland ducts; inserted on the retractor apodeme of the claw. These muscles correspond to branches, a, b, c, d, and e of the retractor of the claws as described by Calora (1957).

15. The ventral retractors of the claws (*vrn*); a broad fan of

muscles originating caudad of 13 on the body wall but below the slime gland duct and inserted on the retractor apodeme.

Such evidence concerning the homologies of the feeding claws as given above would be inconclusive were it not supported by the evidence of embryonic development. Here, too, investigators who have worked on the development of this form are in disagreement. Unfortunately no material was available for a study of this kind. Consequently one must rely on the works of others for information on head development. Of those who have published on the embryology of *Peripatus*, Pflugfelder (1948) and Manton (1949) have worked most recently, and it is mainly from their papers that the following account has been taken.

DEVELOPMENT OF THE EMBRYO

The entoderm and mesoderm of *Paraperipatus amboinensis* originate separately from cells proliferating inwardly from the ventral part of the blastoderm according to Pflugfelder. The entoderm appears first and forms in a short time an inner lining which becomes one cell in thickness except where the cells bunch up at the zone of proliferation (fig. 4 E, *Ent*). This point of proliferation is flanked by tall, slender cells known as fibroid cells (*Fz*). A groove forms beneath this zone in the early gastrula stage which Pflugfelder calls the primitive groove. He purposely avoids the term "blastopore," for he says, "such a porus appears nowhere during the fetal development of *Paraperipatus amboinensis*." This groove apparently corresponds to the early transient blastopore noted by Manton. The development of the endoderm continues long after the majority of coelomic pouches have appeared (fig. 4 G).

The formation of the mesoderm, like the formation of the entoderm, takes place at a spot closely behind the primitive cavity, being formed from the beginning in pairs. The right and left immigrating zones are separated by median fibrous cells (fig. 4 F). At the points of proliferation, the cells accumulate as domelike invaginations, but laterally they thin out into single cell layers which push between the entoderm and the ectoderm (fig. 4 F, *Mes (lat)*). Even in these dome-like masses the cells have a tendency to arrange themselves into a single layer which causes the coelomic cavities to form (*Coel*).

An undifferentiated mesodermal band does not appear in the head region in front of the primitive cavity; the immigrated mesodermal material rather differentiates close to its place of origin into the paired coelomic pouches and into the further proliferating lateral mesoderm.

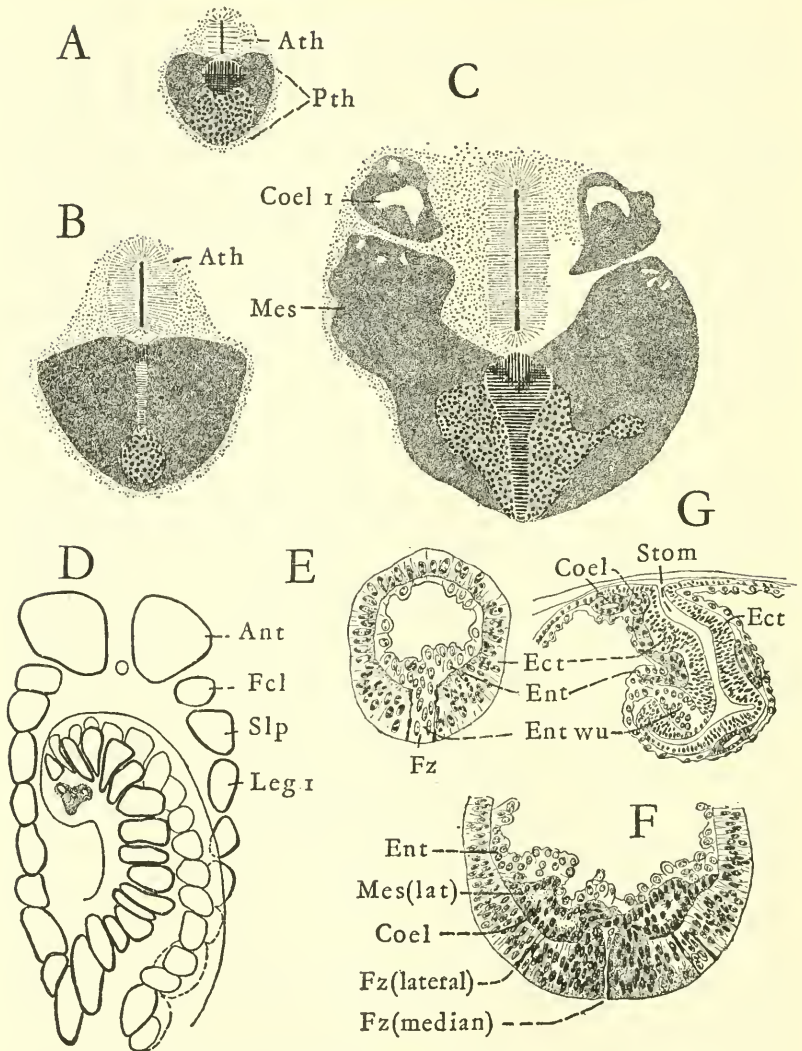


FIG. 4.—Embryonic development of endoderm and mesoderm.

A, B, C, 3 stages of the development of germinal disc of *Peripatopsis mosleyi* (adapted from Manton). D, late stage in development of coelomic sacs, *Peripatopsis mosleyi* (adapted from Manton). E, F, G, stages in development of mesoderm and endoderm in *Paraperipatus amboinensis* (adapted from Pflugfelder).

Ant, coelomic sacs of antennal segment; *Ath*, anterior thickening (Manton); *Coel*, coelomic cavities; *Ect*, ectoderm; *Ent*, endoderm; *Entwu*, point of proliferation of endoderm (Pflugfelder); *Fcl*, coelomic sac of feeding claw segment; *Fz*, fiber cells (Pflugfelder); *Mes*, mesoderm; *Pth*, posterior thickening (Manton); *Slp*, coelomic sacs of slime papillae; *Stom*, stomodaeum.

Through the longitudinal growth of the ectoderm the coelomic pouches are passively removed from the place of their origin; i.e., from the very beginning they remain connected with that point of the germ band to which they belong functionally, according to Pflugfelder.

In some species the blastopore and thus also the point of proliferation of the mesoderm remain at the posterior end of the body. According to Manton, at the stage when the germ band forms on the surface of the blastoderm, two germinal discs occur, in various species of *Peripatopsis* worked on by her, as separate thickenings of the blastoderm. The posterior thickening (*Pth*) arises first, followed quickly by an anterior thickening (fig. 4 A, B, *Ath*). The posterior thickening (*Pth*) gives rise to the blastoporal area from which the mesoderm is formed in all species described by her, and from which in some species the entoderm is also formed. The anterior thickening gives rise to the ectodermal part of the lips of the mouth-anus (fig. 4 A, B, *Ath*) and later to the midventral ectoderm of the body.

The proliferating mesoderm forms a U, with the arms pushing in an anterior direction around the anterior thickening (fig. 4 C, *Mes*). When the arms reach the halfway mark along the mouth-anus, the anterior portions of each arm break away, become hollow, and form the coelomic sac of the first somite (fig. 4 C, *Coel 1*). As the arms continue to push forward, succeeding somites are formed in a like manner. In the meantime the groove forming the mouth-anus has elongated and the middle edges have grown together, leaving only the mouth and anal openings which become ever more widely separated as the embryo grows in length. Figure 4 D shows the embryo with the last pair of coelomic sacs separating from the mesodermal band, after which the mesodermal band soon disappears.

Manton says of the anterior sacs, "The first pair approach each other anterior to the mouth and establish the antennal segment. The second pair are smaller and lie at the side of the mouth where they establish the mandibular segment. The third pair are larger than the second and all succeeding somites in early stages in some species . . . and establish the slime papilla segment."

As for the development of the nerve cord we must turn to Sedgwick (1885), Kennel (1888), and to Pflugfelder, since Manton does not discuss this important phase of development in her paper. The nerve cord of *Paraperipatus amboinensis* according to Pflugfelder develops from paired thickenings on the ventral side of the embryo.

These ridges become segmented as the result of concentrations of ganglion cells, and the resultant lobes are known as the ventral organs.

Unfortunately Pflugfelder does not figure them in whole mounts in his paper, but Sedgwick (1885) for *Peripatus capensis*, and Kennel (1884, 1888) for *Peripatus edwardsi* and *Peripatus torquatus*, show the arrangement of the ventral organs very clearly from the ventral side. Figure 5 A of *Peripatus capensis* illustrates an early stage in the development of the ventral side of the embryo. In this figure, though the lips of the oral cavity are already forming, the appendages of the second visible segment which will become the feeding claws are still located laterally. Adjacent to them the lobes that will form the feeding claws are evident, and the relationship of the future feeding claws to this segment is unmistakable. In figure 5 B the lips have become much more extensive and the feeding claws have begun to withdraw into the preoral cavity and with them the ventral lobes of the second segment. The antennae and the antennal lobes are distinctive from the first, and the appendages of the segment following that of the feeding claws show by the presence of the forming orifice that they will become the slime glands. Figure 5 C shows the ventral organs lying adjacent to each other along the center line. The segments indicated in these three figures, therefore, are the antennal with the largest ventral lobes, the segment of the feeding claws with ventral organs that become much smaller as the embryo develops, and the segment of the slime glands.

Figure 5 D has been adapted from Kennel and shows a slightly later stage of *Peripatus edwardsi*. Here the feeding claws and the ventral lobes of the feeding claw segment have withdrawn completely into the oral cavity, the large anterior ventral lobes are the antennal lobes; those immediately caudad of the preoral cavity are the lobes of the papillar segment. The large dorsal lobe of the oral lips is distinct in this figure.

At least at the time of their origin the ventral organs show a striking similarity to the developing neural ridges of some beetle embryos, as a study of these figures indicates. However, some significant differences soon appear. In the first place nerve cells do not form from neuroblasts in the ectoderm as in insects, but instead cells of the organs migrate through the inner "basement membrane" to form the nerve cord, and as they continue through the membrane, the ventral organ shrinks in size and finally disappears. Only those of the antennal segment are retained and appear on the under side of the adult brain as the hypocerebral organs (fig. 2 A).

According to Evans (1902) the brain also includes a pair of anterior archicerebral lobes belonging to the anterior extremity of the head, and Pflugfelder by means of serial sections was able to demon-

strate the presence of two widely spaced but much smaller ventral organs lying anterior to and underneath the antennal lobes. However, these anterior ventral organs apparently never reach a size suffi-

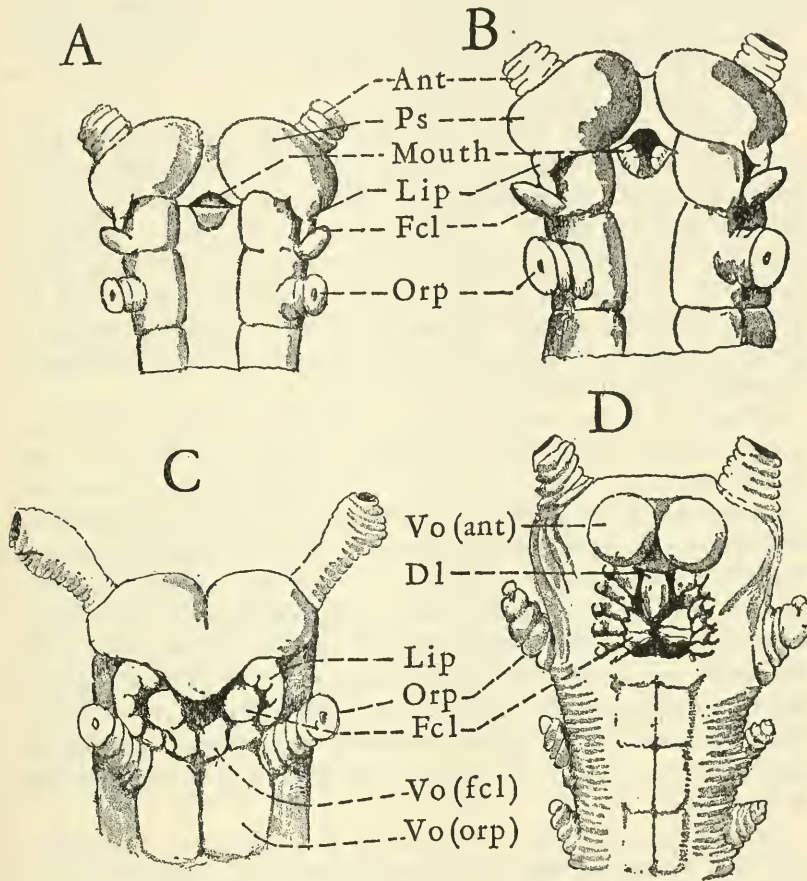


FIG. 5.—Development of onychophoran head.

A, B, C, stages in development of *Peripatus capensis*, adapted from Sedgwick. D, older embryo of *Peripatus edwardsi*, adapted from Kennel.

Ant, antenna; *Dl*, dorsal lobe; *Fcl*, feeding claw; *Orp*, oral papilla (Sedgwick); *Ps*, preoral somite (Sedgwick); *Vo*, ventral organ.

cient for them to be seen in whole mounts of the embryo, since they have not been reported by previous workers. Thus the brain appears to be composed of three ganglionic centers, the optic lobe, the antennal lobe, and a third pair of lobes with nerves given off to the stomodaeum and the feeding claws. According to Pflugfelder, Plate in 1922 recog-

nized this arrangement, and he further homologized the feeding claws with the second antennae of the Crustacea and the slime papillae with the mandibles of the Crustacea, the Myriopoda, and the Insecta. Such an interpretation of the third brain with its nerve connections running to the feeding claws is in accord with the opinions of many authors, among them being Manton (1949), Holmgren (1916), Hanström (1935), Henry (1948), and others.

However, Federov (1929) considers that the brain consists of the prostomial archicerebrum and of postoral elements consisting of the antennal centers, the premandibular centers, the mandibular centers, and the papillar centers. Snodgrass says of his work, "Federov's elaborate analysis of the brain structure and nerves would be more convincing if it took into account the embryonic development of the brain; his results are entirely unsupported by ontogenetic evidence, and are mostly at variance with observations on the brain development reported by other investigators."

Pflugfelder in his study on the development of *Paraperipatus amboinensis* gives considerable evidence in support of Federov's idea and illustrates his findings by a series of reconstructions of cross sections through the head region. The third or tritocerebral segment he considers to be anterior to the jaw or mandibular segment, and anterior to the commissure of the jaw or mandibular segment, he finds another one which he considers to be the first postoral commissure. His theories have been supported by Weber (1952) who says in his discussion of Henry's and Pflugfelder's papers, "It [Henry's opinion that the mandibular nerve belongs to the tritocerebrum] . . . is nevertheless erroneous and Pflugfelder refuted Miss Henry's opinions in advance without having known her work published at the same time as his."

Despite these opinions of Pflugfelder that appear to support Federov, and Weber's acceptance of the idea that a premandibular somite exists in the Onychophora, there are several factors that one must consider before accepting Pflugfelder's work. In the first place in the stages preceding the formation of the preoral cavity one may plainly see that the feeding claws are the appendages of the segment immediately behind the antennal segment (fig. 5 A, B, C), that they are adjacent to the second ventral organs, and that there is no extra coelomic sac between the segments of the antennae and of the feeding claws (fig. 4 D).

It is evident that Pflugfelder used an advanced embryo of *Paraperipatus amboinensis* in making the series of cross sections upon which he based his conclusions. The preoral cavity has formed and the feed-

ing claws have withdrawn into this cavity. Also a cephalic movement, accompanied by a dorsal movement, of the ventral organs around the stomodaeum has commenced. This leads to alterations in position and even to distortion of the ventral organs involved. I, therefore, feel that placing full reliance upon such sections is not justified.

Pflugfelder's efforts to prove the presence of a premandibular segment would be more acceptable if he had found such a segment at an earlier stage before the preoral cavity had begun to form.

Both Pflugfelder and Federov apparently base their theory of head segmentation in the Onychophora on the assumption that the feeding claws are true mandibles, and the necessity to interpolate another segment between the antennal and the mandibular segments has led them into complicated reasoning that is hard to follow. The earliest stages in which segmentation appears have always been accepted as the stages that determine segmentation in any form, and the Onychophora should not be considered as exceptions to this rule.

SUMMARY

The head of *Peripatus* is an undifferentiated region without grooves to mark its segmental areas. The head appendages are the antennae, the feeding claws, and the slime papillae. There is no labrum, the preoral cavity being surrounded by oral lobes constituting the lips, the dorsal lobe of this group forming a structure similar to the epipharynx of insects. The dorsal lobe aids in the ingestion of food. The feeding claws are not homologous with mandibles but rather correspond to the transitory labral lobes found in some insect embryos. This is indicated by the following facts:

1. They are innervated by the third or tritocerebral segment of the brain.
2. They do not function as mandibles or chewing jaws but more as scratching claws.
3. The coelomic sacs of the feeding claw segment are located immediately behind the antennal coelomic sacs.
4. The ventral organs of the feeding claw segment form the third or tritocerebral lobes of the brain.
5. The feeding claws do not form from ental lobes of the basal leg segments as in insects, but are simply greatly strengthened claws developed from a much altered walking leg.

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THE EXTERNAL ANATOMY OF THE SOUTH
AMERICAN SEMIAQUATIC GRASSHOPPER
MARELLIA REMIPES UVAROV (ACRID-
OIDEA, PAULINIIDAE)

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(WITH ONE PLATE)

FOREWORD

Very nearly 20 years ago I bought, on the advice of an elder colleague, a copy of Snodgrass's "Principles of Insect Morphology." I had already been interested for many years in the insects, but Snodgrass's book opened for me a new horizon in their study. By laborious reading in a language with which I was not then familiar, I learned many things about the structure of insects and how they function as living mechanisms, and conceived an unlimited admiration for the author of the book.

Later I sought an opportunity of going to the States to study entomology, and for some time enjoyed the rare privilege of being the disciple of the author of that notable book. What for years had appeared to be an unattainable utopia came true, and for many months I worked in morphology under his kind and patient guidance. If the reading of his books had made me admire Snodgrass, working by his side awakened in me the warmest affection for the kind and unassuming man I found him to be.

Through the years, after my return to Uruguay, Snodgrass has continued by his personal letters to encourage me in my work, to give advice, and by his published works to enlighten my mind in scientific matters. This little work on the anatomy of a South American insect is intended as a contribution to a volume to be dedicated to Snodgrass. The contents of this modest contribution may not prove to be worthy of the circumstances, but, being a piece of my own personal work, is the best I can offer to thank and honor Dr. Snodgrass.

C. S. C.

Montevideo, October 1957.

INTRODUCTION

The South American semiaquatic grasshopper *Marellia remipes* was described by Uvarov (1929) from a single female specimen from Paraná (province of Entre Ríos, Argentina) sent to him by Dr. Carlos A. Marelli. Several closely related species of the same genus were subsequently discovered in different parts of South America: *Marellia clearei* Uvarov, 1930, from British Guiana; *M. paludicola* Guenther, 1940, from eastern Perú, and *M. geyskeia* Willemse, 1948, from Surinam. The male of *Marellia remipes* was described almost simultaneously by Liebermann (1940) and Rosas-Costa (1940) more than a decade after Uvarov's description of the female.

In his original description of *Marellia remipes*, Uvarov (1929) states that this newly discovered genus of insects presents obvious adaptations to semiaquatic life, as revealed by the remarkable expansion of the hind tibiae. He also points out the peculiar structure of the apical portion of the abdomen and the ovipositor, remarking that they suggest a very unusual habit of oviposition.

A number of authors have published later reports on this curious genus of grasshoppers, or have made reference to it in general works of acridiology. Uvarov (1930), Chopard (1938), Liebermann (1940), Rosas-Costa (1940), Rosillo (1940, 1941), and Willemse (1948), verify the semiaquatic habits of *Marellia*, stating that the insects live on aquatic plants and swim easily, both on the surface and under water, being able to spend considerable time submerged among the aquatic plants, to the stems of which they cling to avoid floating back to the surface.

Of the papers referred to in the preceding paragraph, those of Rosillo (1940) and Willemse (1948) are particularly illustrative of the habits of the insects of this genus. Rosillo observed *Marellia remipes* near the city of Paraná (Entre Ríos, Argentina) living on aquatic plants in shallow waters of the Paraná River. According to this author, the plant preferred by the insect at this particular place is *Hydromystria stolonifera* May. (Hydrocharitaceae), a plant with round or oval floating leaves on which the insects live and feed. He describes for the first time the peculiar feeding habits of these insects, which gnaw holes on the surface of the leaves instead of eating them from the edges as do other grasshoppers.

In the other paper Willemse transcribes observations on *Marellia clearei* communicated to him by Dr. D. C. Geyskes of Paramaribo

(Surinam). According to this observer, *M. clearei* lives on the floating leaves of the water lilies (probably *Nymphaea*) and feeds on them. He, too, mentions the unusual way in which the leaves are eaten from their surface and describes the peculiar aspect of the partially eaten leaves, so characteristic as to betray the presence of the insects before they can actually be seen. In this very interesting paper, Willemse figures the mouth parts, wings, and external genitalia of *M. clearei*.

The present writer (Carbonell, 1957) has recently published an account of the habitat, activities, and oviposition of *Marellia remipes*, which he found living on aquatic plants in shallow, permanent ponds near the bed of the Cuareim River and affluents in northern Uruguay. The insects live there on the floating leaves of the water poppy, *Hydrocleis nymphoides* Willd. (Butomaceae), on which they preferably feed. The leaves of the plant are eaten in the same way as described by Rosillo (1940) and Willemse (1948), i.e., directly from their upper surfaces and never from the edges. An aspect of the habitat of *M. remipes* in Uruguay is shown in plate 1, where some partially eaten leaves of the water poppy can be seen. As Willemse indicates, the very aspect of these leaves is so characteristic as to reveal from a distance the presence of the insects. In the present writer's 1957 paper, he confirms the observations already mentioned on the swimming of the insects on the surface and under water, where they seek shelter and hide for considerable periods of time among the submerged stems of the aquatic plants. The egg pods of *M. remipes* are described in that paper for the first time. They were found entirely submerged in the water, adhering to the undersurface of the floating leaves of the host plant.

With reference to the host plants of the genus *Marellia*, it must be remarked that those preferred by the species *remipes* belong to nearly related families, while the water lilies on which *clearei* feeds belong to one that is entirely unrelated to the other two. All these plants, however, share a common characteristic: their leaves float horizontally on the surface of the water, this circumstance being apparently a decisive factor in determining the suitability of the plant to the needs of the insects.

The authors who have written on *Marellia* and *Paulinia*, the only genera of the family, have invariably remarked that these insects present striking adaptations to the semiaquatic habitat. From an anatomical viewpoint, they show notable adaptations to aquatic locomotion in the structure of the tibiae, tibial spurs, and tarsi of the hind legs. The structure of the hind legs has earned for the first described

species of *Marellia* the specific name of *remipes*, or oar-shaped legs. The unusual structure of the ovipositor has for a long time been regarded as a further anatomical adaptation to the aquatic habitat, though it was not until recently (Carbonell, 1957) that the meaning of this modification of the egg-laying organ was ascertained. Even more striking than these structural adaptations are, in the writer's opinion, the corresponding adaptations in behavior, such as the habit of swimming under water and the very peculiar oviposition habits.

The study of the external anatomy of *Marellia remipes* has made evident to the writer that the aforementioned adaptations are not the only ones to be found in this remarkable insect, which is also structurally modified for its life on the horizontal surface of the floating leaves of the host plants, and for feeding on them from their upper surfaces. Though a phytophilous grasshopper in the strict sense of the word, the general depressed shape of its body, the position of its eyes on the upper part of the head, and the reduction of its pretarsal arolia are features characteristic of the geophilous forms. This may be interpreted as a convergence produced by the life upon a horizontal surface, but if the Pauliniidae are phylogenetically related to the Ommexechidae, as the study of the phallic complex of these families has suggested to Dirsh (1956), then the presence of these features in the Pauliniidae will not be just a case of convergence with the geophilous Ommexechidae, but will reveal instead, a community of ancestry. Paradoxically enough, the eminently geophilous and xerophyllic Ommexechidae would have their nearest relatives living in an aquatic habitat, never coming to land except by accident.

The fact that the immense majority of the Acridoidea are inhabitants of dry land, and many of them distinctly xerophyllic, suggests that the invasion of the aquatic habitat by a few species of them must be a secondary event in the history of these insects. If the degree of adaptive modifications to an unusual habitat attained by a certain species can be considered as proportional to the length of time it has been living in this particular habitat, then we are led by the study of the external structure of the Pauliniidae to regard them as the representatives of the earliest group of grasshoppers that made aquatic plants their permanent abode.

In the description of the external anatomy of *Marellia remipes* that follows, the writer has borne in mind that the structure of several species of grasshoppers has been described carefully and in great detail, and therefore he has limited his account to the description of those features of the insect that reveal adaptations to its habitat, or of

the structures that appear to him to be different from those of the previously described species.

Acknowledgments.—The present work is the result of research performed by the author in the Universidad de la República, Montevideo, Uruguay. It was done almost entirely in the Insectary Section of the Facultad de Agronomía and was based on specimens belonging to the Laboratory of Entomology of the Facultad de Humanidades y Ciencias and collected on field trips organized by the Laboratories of Vertebrate Zoology and Entomology of this College.

The writer acknowledges his deep gratitude to Dr. R. E. Snodgrass for the much needed correction of the style of the manuscript. He also wishes to thank Dr. B. P. Uvarov, who made available his bibliography on the subject and made useful suggestions on the work to be done.

I. GENERAL FORM OF THE BODY

Marellia remipes (fig. 1) is a stout-bodied grasshopper of medium size. Its antennae are relatively short, and its hind legs are strong and well developed. The males are of a somewhat more slender build than the females, and their dimensions are slightly smaller.

The body of these insects is depressed and, the upper part of it being considerably narrower than the sternal region, its lateral walls slope downward and outward from the dorsum to the broader venter. A transversal section through the thorax of the insect appears shaped like a trapezoid, with its broader base down, this base being noticeably larger than the height of the figure.

In the phytophilous grasshoppers, the body is usually compressed instead of depressed. Though the sternal region is often in them, too, broader than the tergal one, this condition is never so marked as in *Marellia*. In this respect, the general aspect of *Marellia* resembles that of the geophilous South American Ommexechidae, in which the depressed shape of the body and the exaggerated width of the sternal region, particularly in the pterothorax, are even more marked.

Among the populations of *Marellia remipes* studied by the writer in northern Uruguay, brachypterous (fig. 1 B) and macropterous (fig. 1 A) forms were found together, the former being about twice as abundant as the latter (Carbonell, 1957).

II. THE HEAD AND THE MOUTH PARTS

The head of *Marellia remipes* is shown in figure 2. It agrees in general with the descriptions given of the head of other grasshoppers, but shows, too, some peculiarities of its own. It is somewhat conical

in shape, and the frontoclypeal region slopes downward and rearward to the labrum. The frontal costa is broad around the median ocellus, narrowing upward to the vertex and becoming indistinct down from the subantennal suture (fig. 2, *j*). The frontal carinae (*i*) consequently are well marked on the upper part of the head from the vertex to the subantennal suture, where they disappear.

The eyes and ocelli.—The ocelli (fig. 2, *O*) are rather large. The compound eyes (*E*) are relatively small, globose, prominent, and situ-

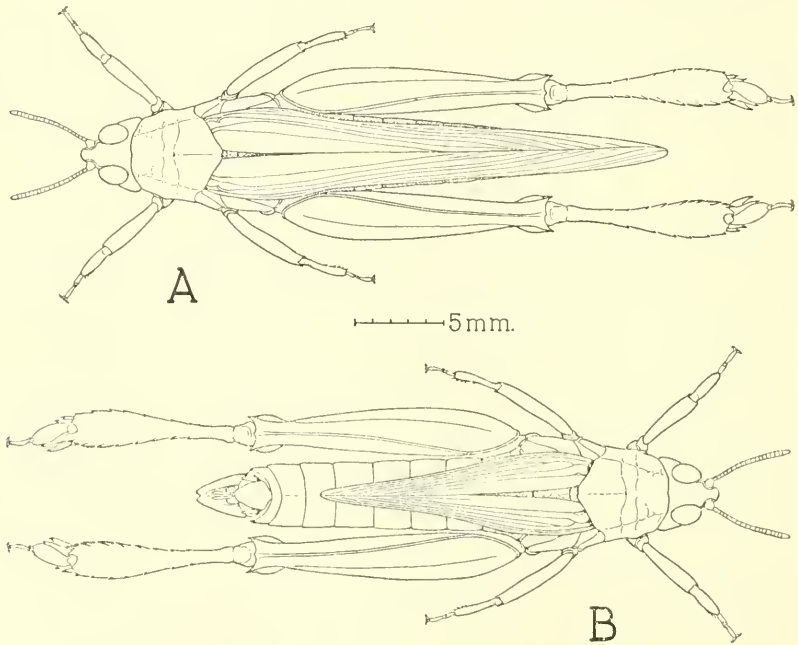


FIG. 1.—*Marellia remipes* Uvarov, female, dorsal view.

A, macropterous form. B, brachypterous form.

ated on the upper lateral regions of the head. Phytophilous grasshoppers in general show larger compound eyes, more elongated toward the genal region of the head, and usually not so prominent as in *Marellia*. The form and situation of the compound eyes again recall the geophilous Ommexechidae, in which they are globose and similarly situated on the upper part of the head.

The antennae.—The antennae (fig. 2 A, *Ant*) are relatively short, with a scape and pedicel well differentiated. The diameter of the flagellum slightly increases from its insertion on the pedicel to the apical segment.

The clypeus, labrum, and epipharynx.—The clypeolabral region of the head (figs. 2, 5, *Clp*, *Lm*) does not differ much from the same region in other grasshoppers. The clypeus (fig. 2, *Clp*) is distinctly separated from the frons by a frontoclypeal or epistomal suture (*es*). Its limit with the labrum is similarly marked by the clypeolabral suture. The labrum is slightly asymmetrical, this asymmetry being more noticeable from its posterior or epipharyngeal surface (fig. 5 A) because of the irregular distribution of the bristlelike hairs that cover

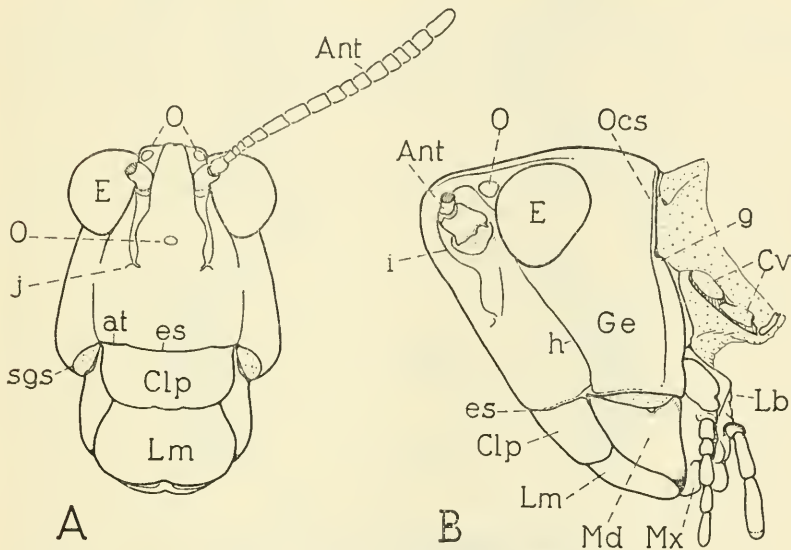


FIG. 2.—The head of *Marellia remipes*.

A, anterior view (palpi not drawn). B, lateral view.

Ant, antenna; *at*, anterior tentorial pit; *Clp*, clypeus; *Cv*, cervical sclerites; *E*, compound eyes; *es*, epistomal suture; *Ge*, gena; *h*, subocular ridge; *i*, frontal carina; *j*, subantennal suture; *Lb*, labium; *Lm*, labrum; *Md*, mandible; *Mx*, maxilla; *O*, ocellus; *Ocs*, occipital suture; *sgs*, subgenal suture.

some of its surface. The tormae (*Tor*) are clearly visible in the limit of the clypeus.

The mandibles.—The mandibles of *Marellia remipes* (fig. 3) are, as in all grasshoppers, asymmetrical, the left mandible being larger than the right one and broadly overlapping it when closed. The masticatory or mesal edge of each mandible is differentiated into a molar area (*ma*) and an incisor lobe (*il*). As far as these features are concerned, the mandibles of *Marellia* follow the general structure of the grasshopper mandible. There are, however, several details that will be referred to below, which are peculiar to this particular insect.

Acridoid mandibles have been classified in three main types (Isley, 1944,¹ Williams, 1954), which are correlated with the type of food plants preferred by the insects. The mandibles of the grass-eating or graminivorous grasshoppers have the incisor lobes provided with blunt teeth, and the molar areas formed by a series of ridges and furrows. In this type, the left mandible only slightly overlaps the right one.

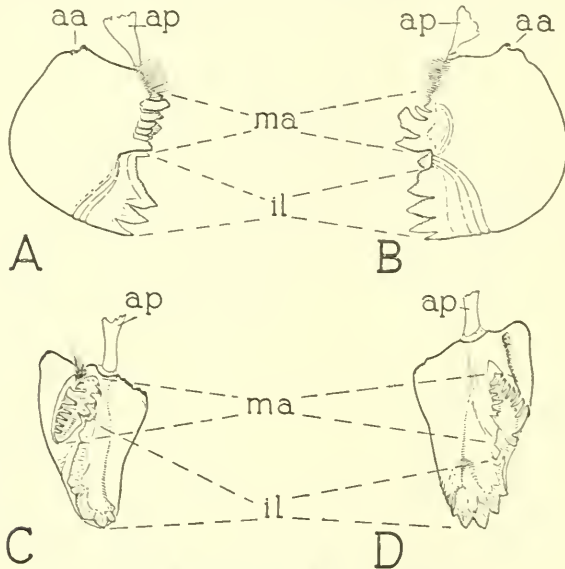


FIG. 3.—Mandibles of *Marellia remipes*.

A, right mandible, anterolateral view. B, left mandible, anterolateral view. C, right mandible, mesal view. D, left mandible, mesal view.

aa, anterior articulation of mandible; *ap*, adductor apodeme of mandible; *il*, incisor lobe; *ma*, molar area.

The mandibles of grasshoppers that feed on broad-leaved plants—which have been called the herbivorous or forbivorous type—present an incisor lobe armed with pointed, sharp-edged teeth, and their molar areas consist of several pointed teeth around a central cavity. In the herbivorous type of mandibles, the left considerably overlaps the right one.

The third or intermediary type occurs in the grasshoppers that feed on either type of plants, and their characteristics are intermediate.

¹ Isely, F. B., Correlation between mandibular morphology and food specificity in grasshoppers, *Ann. Ent. Soc. Amer.*, vol. 37, pp. 47-67, 4 figs. 1944. The present writer has not seen this work and cites it through references made by Uvarov (1948) and Williams (1954).

The mandibles of *Marellia* (fig. 3), which is a typical broad-leaved plant feeder, belong very definitely to the second or herbivorous type. The teeth of the incisor lobes (*il*) have their edges extraordinarily sharp and minutely jagged. The molar areas (*ma*) are armed with very prominent marginal teeth, especially on the left jaw, where the anterior part of the molar area shows two very long, upcurved teeth with jagged edges. In this insect the left mandible (B, D) is noticeably larger than the right one and broadly overlaps it when closed.

The mandibles of *Marellia remipes* show, however, some features that depart from the straight herbivorous type, which are correlated with the unusual mode of feeding of these insects. As has been stated in the introductory part of this paper, *Marellia* does not eat the leaves from the edges, but gnaws holes on their surface instead. Sometimes these holes do not come through the leaf, but only the upper parenchyma is eaten, leaving the network of veins, and the aerenchyma below, intact. Commenting on this unusual way of feeding, Uvarov (personal letter) pointed out to the writer that the study of the mouth parts of the insects would surely disclose special adaptations to this type of feeding. This inference proved to be true, since it can be seen in the jaws of *Marellia* that the incisor lobes (fig. 3 C, D) are strongly curved rearward, in such a way that when the insect stands on a leaf of the host plant and lowers its head for feeding, it is not the apical end of the incisor lobe that comes in contact with the leaf surface, as would happen if it were straight, but a considerable length of the convex toothed edge instead. In this way the sharp, jagged edges of the incisor lobes are able to cut superficial pieces from the flat leaves, and the insect does not need to attack them from their edges, which in the case of floating leaves would be, if we can use an anthropomorphic word, impractical.

Marellia is not, however, the only grasshopper that eats in this particular way. A similar way of feeding on the broad leaves of the water hyacinth (*Eichhornia azurea*) by the grasshopper *Cornops aquaticum* Br. has been reported by Covelo de Zolessi (1956).

The maxillae.—The maxillae of *Marellia remipes* (fig. 4 A, B) have the usual structure of the grasshopper maxillae, as it has been described by Snodgrass (1928). The cardo (*Ca*) is roughly triangular; the stipes (*St*) is quadrate, with a differentiated palpifer (*Pf*). The maxillary palpi are five-segmented. The galea (*Ga*) is membranous and relatively narrow, and the lacinia (*Lc*) armed with a number of very sharp apical teeth. The maxillae are slightly asymmetrical in shape.

The labium.—As do the maxillae, the labium (fig. 4 C) conforms to the typical acridoid structure. The submentum (*Smt*) is large, with elongated basal angles. The broad mentum (*Mt*) carries laterally the three-jointed labial palpi (*Plp*), and apically the large paraglossae (*Pgl*) and the very small glossae (*Gl*).

The hypopharynx.—The hypopharynx (fig. 5 B, C) does not show major differences from that of other grasshoppers. Its lateral and

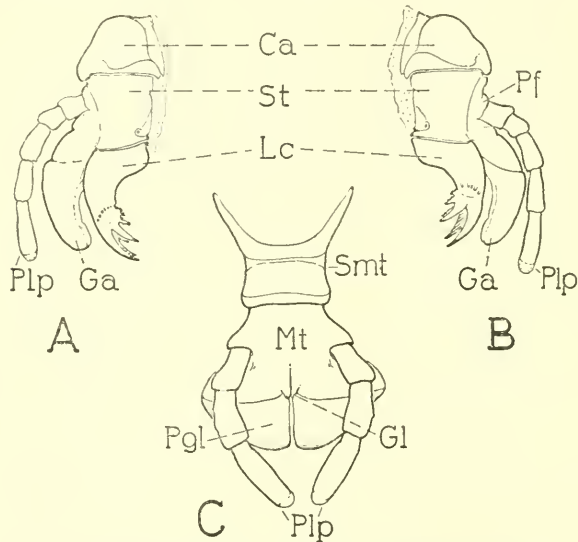


FIG. 4.—Maxillae and labium of *Marellia remipes*.

A, left maxilla, posterior surface. B, right maxilla, posterior surface. C, labium, posterior view.

Ca, cardo; *Ga*, galea; *Gl*, glossa; *Lc*, lacinia; *Mt*, mentum; *Pf*, palpifer; *Pgl*, paraglossa; *Plp*, palpus; *Smt*, submentum; *St*, stipes.

posterior surfaces (fig. 5 C) are covered by rather large sclerotized plates.

III. THE THORAX

As can be seen in figure 1, the thorax of *Marellia remipes* is wide and depressed, narrowing upward from a broad sternum to its tergal region. Seen from above, the thorax is narrowest at the anterior edge of the prothoracic region, broadening gradually from there backward to the line passing through the anterior edges of the cavities of the hind coxae.

The prothorax.—The general shape of the prothorax is illustrated in figures 1 and 6. It is relatively short, considering the size of the

insect. Its articulation with the head comprises the usual cervical sclerites (fig. 2, *Cv*) in the membranous wall of the neck region.

The protergum (fig. 6, *T*) has a slightly convex upper surface or disc, which turns abruptly down along definite lateral lines to form the ample lateral lobes. The disc of the protergum shows two well-marked grooves which are continued along the lateral lobes, nearly to their edges.

The visible part of the pleural region, the prothoracic sternum, and the articulation of the forelegs do not offer any peculiarity of their own. The prosternum (fig. 9, *S*₁) lacks the spine-shaped tubercle present in other grasshopper families.

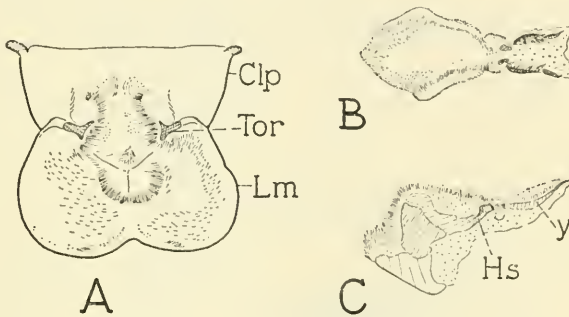


FIG. 5.—Clypeus, labrum-epipharynx, and hypopharynx of *Marellia remipes*.

A, clypeus and labrum, posterior view showing epipharyngeal surface. B, hypopharynx, anterior view. C, hypopharynx, lateral view.

Clp, clypeus; *Hs*, suspensorial bar of hypopharynx; *Lm*, labrum; *Tor*, torma; *y*, oral branch of suspensorial bar of hypopharynx.

The pterothorax.—The pterothoracic region in *Marellia* is, in its general structure, similar to that of other described species of grasshoppers. In brachypterous and macropterous specimens some differences in the degree of sclerotization can be noticed in the articulation of the wings and in the metathoracic tergum. In general, the axillary sclerites are less well defined, and the desclerotized areas between the scutum and the scutellum of the metathoracic tergum are smaller in the short-winged forms.

The tergal region of the pterothorax (fig. 7) is nearly identical with that of *Dissosteira carolina* as described and figured by Snodgrass (1929). Among the minor differences shown, there are in the lateral prescutal areas (*Psc*) of the mesothorax (*MsT*) two small, spinose tubercles (*SpT*) of which the function is unknown to the writer. As we shall see later, similarly spinose formations are visible on the third axillary sclerites of both wings.

On the metatergum (*MtT*) there is only one median desclerotized area, which in size and shape varies somewhat in different individuals. This area is generally shaped like an inverted V and, as has been already stated, tends to be smaller in the short-winged form. The lateral desclerotized areas figured by Snodgrass (1929) in the metatergum of *Dissosteira* do not exist in *Marellia*, which in this detail is similar to the corresponding region of *Nomadacris septemfasciata* as figured by Albrecht (1956).

The pterothoracic pleura.—The pleural region of the pterothorax of *Marellia remipes* (fig. 8) is similar to that of *Dissosteira* (Snod-

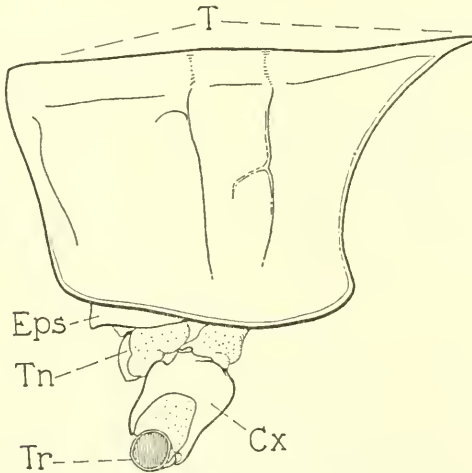


FIG. 6.—Prothorax of *Marellia remipes*, lateral view.

Cx, coxa of prothoracic leg; *Eps*, episternum; *T*, protergum; *Tn*, trochantin; *Tr*, trochanter.

grass, loc. cit.). A remarkable feature, however, is the greater development of the mesothoracic spiracle (*Sp*₂) in *Marellia*, and the hairy covering of the prepectus and adjoining membrane in its vicinity. Considering that this anterior part of the mesothoracic pleural region is covered by the posterior edge of the lateral lobe of the pronotum, it seems highly probable that the mesothoracic spiracle is functional in subaquatic respiration. The hairs on the lateral regions of the prepectus are probably a hydrofugous device for the retaining of air bubbles when the insect is under water, serving as a respiratory supply. As we shall see below, the first and second abdominal spiracles are probably functional too in the submerged insect.

The pterothoracic sterna.—The united sternal plates of the mesothorax and metathorax form the broad ventral surface of the ptero-

thorax (fig. 9), which in *Marellia* is completely flat. The pterothoracic plastron is in this species unusually wide and roughly rhombic in outline. As has already been remarked, the sternal region is by far

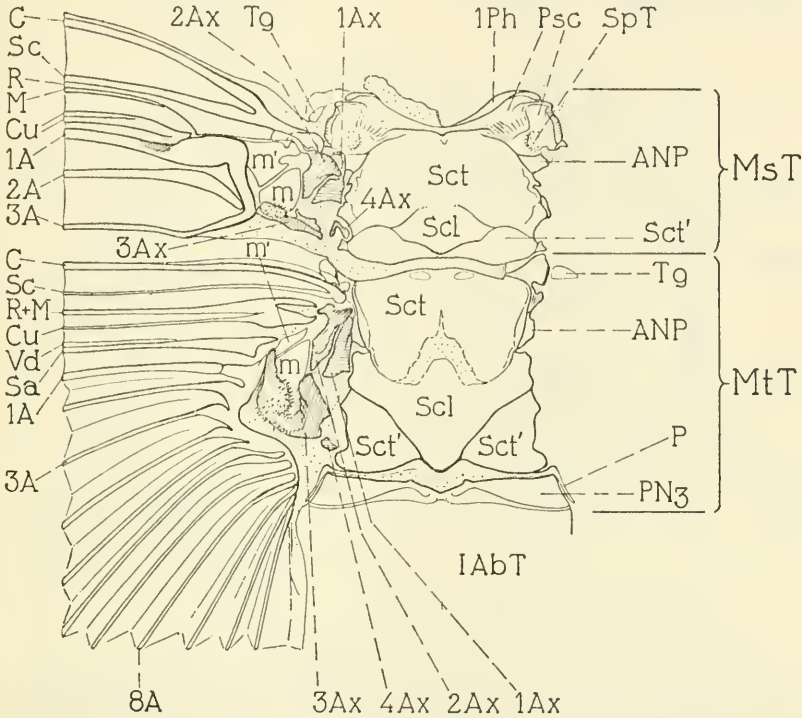


FIG. 7.—The pterothoracic terga and the bases of the wings of *Marellia remipes*.

1A, 2A, 3A, 8A, first, second, third, and eighth anal (vannal) veins; ANP, anterior notal wing process; 1Ax, 2Ax, 3Ax, 4Ax, first, second, third, and fourth axillary sclerites; C, costa; Cu, cubitus; IAbT, first abdominal tergum; M, media; m, m', median plates of wing base; MsT, mesothoracic tergum; MtT, metathoracic tergum; P, tergal arm connected to anal veins of wing; 1Ph, first phragma; Psc, lateral prescutal area; R, radius; R+M, united shafts of radius and media in hind wing; Sa, secondary anal vein; Sc, subcosta; Scl, scutellum; Sct, principal part of scutum; Sct', Sct', posterior, lateral subdivisions of scutum; SpT, spinose tubercle of lateral prescutal area of mesotergum; Tg, tegula; Vd, vena dividens.

the broadest part of the pterothorax, being widest at the anterior margin of the coxal cavities of the hind legs.

The mesosternum shows a curved anterior margin that overlaps the posterior part of the prothoracic sternum. The pleurosternal su-

tures (*pss*) are well marked on it. The coxal cavities of the mesothoracic legs are situated well on the pleural side of the metathorax, instead of being in the more sternal position shown in *Dissosteira* (Snodgrass, 1929), *Nomadacris* (Albrecht, 1956), or *Dociostaurus* (Jannone, 1939).

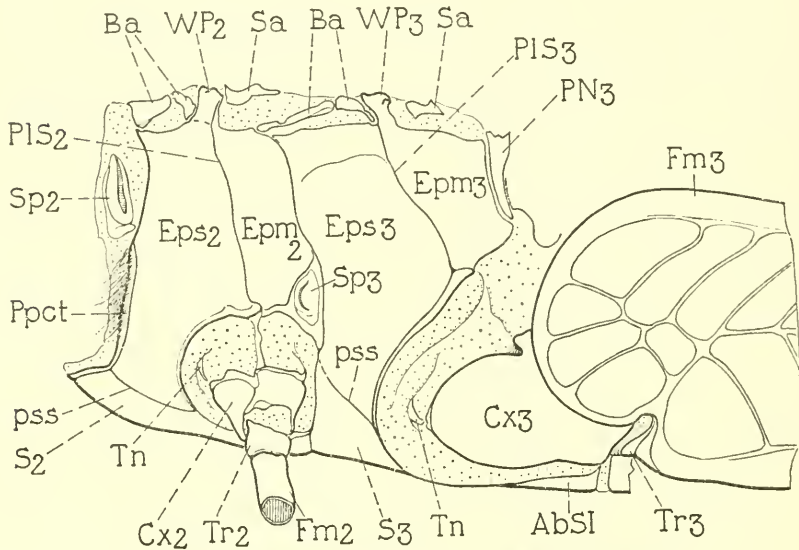


FIG. 8.—The pterothoracic pleura of *Marellia remipes*.

AbSI, first abdominal sternum; *Ba*, basalar sclerite; *Cx*, coxa; *Epm*, epimeron; *Eps*, episternum; *Fm*₃, base of hind femur; *PIS*, pleural suture; *PN*₃, lateral arm of metathoracic postnotum; *Ppct*, prepectus; *pss*, pleurosternal suture; *S*, thoracic sternum; *Sa*, subalare; *Sp*₂, mesothoracic spiracle; *Sp*₃, metathoracic spiracle; *Tn*, trochantin; *Tr*, trochanter; *WP*, pleural wing process.

The metathoracic sternum shows the broad metasternal lobes nearly meeting along the midline, the only visible part of the precostal region of the first abdominal sternum being a rhombus-shaped area between the roots of the sternal apophyses (*sa*). This area is limited anteriorly by the furcal suture (*fs*) and united to the rest of the first abdominal sternum by a very narrow band between the metasternal lobes. The infracoxal lobes of the metasternum that appear well limited by sutures in the three species mentioned in the preceding paragraph are indistinct in *Marellia*, the entire surface of the metasternum being undivided in this species.

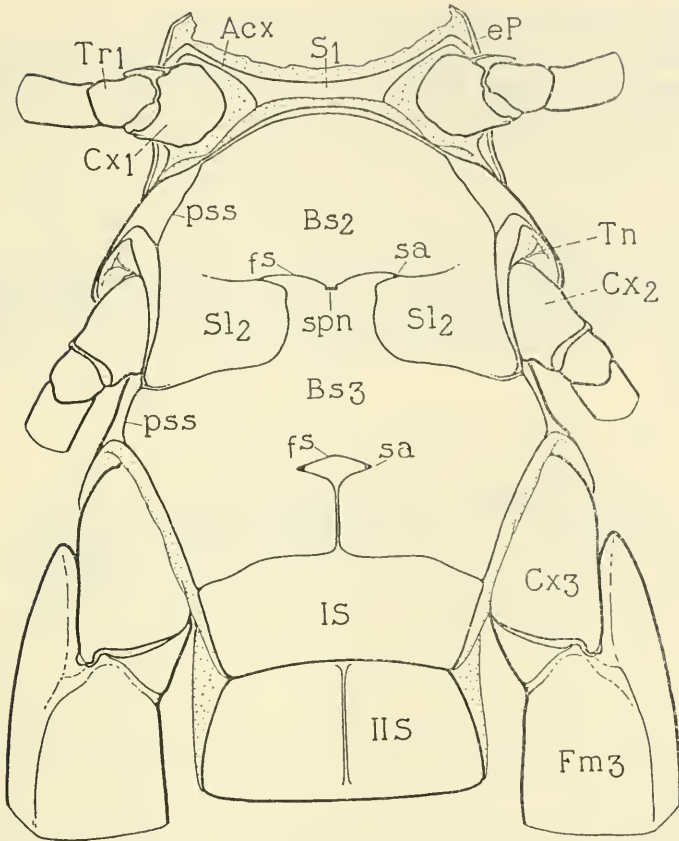


FIG. 9.—Thoracic sternum and base of abdomen of *Marellia remipes*.

Acx, antecostal bridge of prosternum; *Bs*, basisternum; *Cx*, coxa; *eP*, edge of pronotum; *Fm*, femur; *fs*, furcal suture; *pss*, pleurosternal suture; *IS*, first abdominal sternum; *IIS*, second abdominal sternum; *S1*, prothoracic sternal plate; *sa, sa*, roots of sternal apophyses; *Sl*, sternellum; *spn*, depression marking the site of the internal spina; *Tn*, trochantin; *Tr*, trochanter.

IV. THE WINGS AND THEIR ARTICULATIONS

The wings of *Marellia remipes* are figured in a very schematic form in figure 10. The wing venation in this insect, especially in the fore wing, is rather indistinct and obscured by cross-veins, and the writer is not sure of having interpreted it correctly. Wing veins in figure 10 have been named after Snodgrass (1929).

As has been already indicated, there are in this species two forms that differ in the degree of development of the wings. The macrop-terous or long-winged form has its tegmina and hind wings fully

developed; the brachypterous or short-winged form, on the contrary, has both pairs of wings reduced and nonfunctional. The long-winged specimens are perfectly able to fly and they do so, especially at night when attracted by lights. They do not, however, fly readily in the

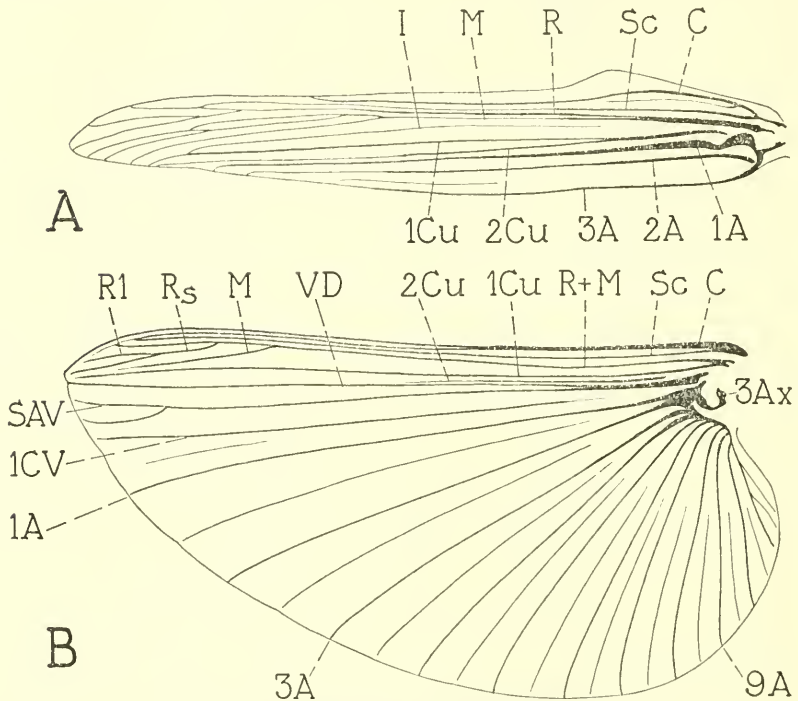


FIG. 10.—The wings of *Marellia remipes*.

A, left fore wing, or tegmen. B, left hind wing.

1A, 2A, 3A, 9A, first, second, third, and ninth anal (vannal) veins; 3Ax, third axillary sclerite; C, costa; 1Cu, 2Cu, first and second cubitus; 1CV, first concave anal vein; I, intercalary vein; M, media; R+M, united basal shafts of radius and media; R, radius; R₁, first branch of radius; R_s, radial sector; SAV, secondary anal vein of first anal plait; Sc, subcosta; VD, vena dividens.

daytime, and when disturbed or chased they usually escape by swimming and submerging as the flightless forms do (Carbonell, 1957).

The tegmen of *Marellia remipes* (fig. 10 A) is narrow and has a pronounced marginal lobe in the costal area, near the base of the wing. When the wings are flexed, this lobe covers the tympanal organ and the first abdominal spiracle, and its development might be related to underwater breathing as we shall see later with respect to the abdominal spiracles.

The hind wing of *Marellia* (fig. 10 B) is well developed in its vanal region. Its remigial region, on the contrary, is narrow and shows a simplified R+M system.

The articulation of the wings.—The articulation of the wings in *Marellia* (fig. 7) does not differ much from the articulation of the wing in *Dissosteira* (Snodgrass, 1929). In both wings the four axillary sclerites (*Ax*) are distinct and so are the median plates (*m*, *m'*). The epipleurites beneath the wing base (fig. 8, *Ba*, *Sa*) are almost identical with those of *Dissosteira*. A curious feature of the articulation of the wing in *Marellia* is the development of bulblike tubercles covered with spiny hairs on the distal parts of the third axillary

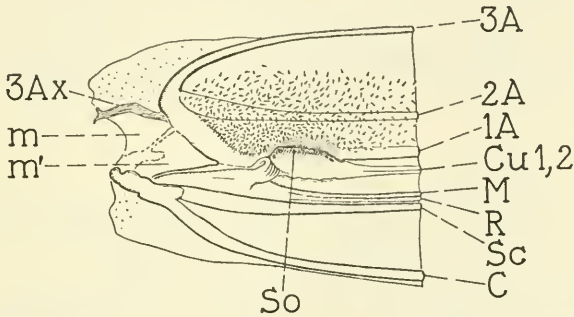


FIG. 11.—Base of right tegmen of *Marellia remipes* (ventral or inferior view), showing the tegminal part of the locking apparatus of the fore wing.

1A, 2A, 3A, first, second, and third anal veins; 3Ax, third axillary sclerite; C, costa; Cu 1, 2, first and second cubitus; M, media; m, m', median plates of the wing base; R, radius; Sc, subcosta; So, socket of the locking apparatus of the fore wing.

sclerites (fig. 7, 3Ax) of both wings. As has been said elsewhere, these tubercles are similar to those of the lateral prescutal areas of the mesothorax (*Spt*), and a study of their microscopic anatomy would be necessary to ascertain their function.

The locking apparatus of the fore wing.—There are on the under-surfaces of the tegmina some structures that, in connection with the second axillary sclerites of the hind wings, form a device that firmly locks the fore wings in their resting or flexed position.

Observing the inferior surface of the basal portion of the tegmen (fig. 11) there can be noticed, at the basal portion of the first anal vein, a fairly deep socket (*So*) surrounded by raised edges. The edge on the anal side of the wing is higher and sharper and projects over the bottom of the cavity. When the wings are flexed in the normal resting position, the very prominent second axillary sclerite of the

hind wing lodges in this socket, securely locking the tegmen in such a way that it cannot be displaced outward unless it is first slightly moved toward the midline of the body and then raised vertically in order to dislodge the mesal edge of the second axillary sclerite of the hind wing from the tegminal socket. The site of this socket near the base of the first anal vein of the tegmen is noticeable from the upper surface as a slightly raised, dark-colored spot. The inferior surface of the basal part of the anal region of the fore wing is covered with spinose hairs which are similar in appearance to those on the tubercles of the prescutal mesothoracic areas and the third axillary sclerites.

The writer believes that the locking apparatus of the fore wing has not been hitherto described. It seems, however, that this structure can be found in other grasshoppers too, since he has observed it in species of the genus *Dichroplus* (Catantopinae). In this last genus, however, it does not seem so well developed as in *Marellia*.

V. THE LEGS

The fore and middle legs of *Marellia remipes* (fig. 12) are similar to those of other grasshoppers. Their femora are somewhat more robust in the male (not figured) than in the female.

A noticeable feature in all the legs of *Marellia* is the poor development of the pretarsal arolia (figs. 12, 13, 14, *Ar*). In spite of its being a phytophilous form, the arolia are not developed as usual in the plant-dwelling grasshoppers, but instead are reduced as in the geophilous forms. The fact that the host plants of this genus have floating leaves that lie in a horizontal position, which makes climbing unnecessary, might be related to the poor development of the arolia. It has already been noted that this feature may possibly indicate a relationship with the geophilous Ommexechidae.

The hind legs.—The hind legs of *Marellia* (fig. 13) are remarkable in several respects and, with the probable exception of the ovipositor, they are the organs of this insect that show the more advanced anatomical adaptations to the semiaquatic habitat.

The coxae (fig. 13, *Cx*) are similar to those of other grasshoppers, being globose, somewhat elongated, and articulated to the thorax by means of a relatively small trochantin (fig. 8, *Tn*). The hind femora (fig. 13, *Fm*) are unusually robust. In fact, the great development of the hind femora is one of the distinctive features in the general aspect of this grasshopper. Aquatic locomotion, it seems, calls for unusual strength of the tibial muscles lodged in the hind femur. The lateral external surfaces of the hind femora are marked with the usual fish-bone

pattern (not shown in fig. 13). On the ventral surface of the basal part of the hind femur, the organ of Brunner in the form of a small, pointed tubercle can be clearly seen in a mesal view of the leg.

The hind tibiae (fig. 13 A, B, *Tb*) are greatly expanded laterally in their apical halves. Seen from its upper surface, the hind tibia (A, *Tb*) is distinctly shaped like an oar or paddle. The whole surface of the distal expanded portion of the tibia has its margins up-curved, so that the expanded part is spoon-shaped rather than simply

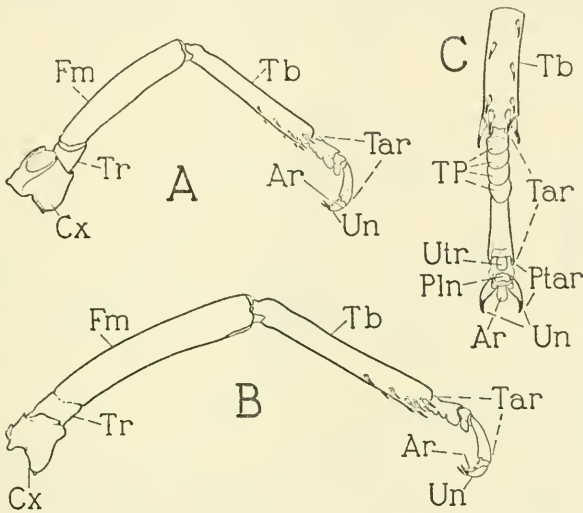


FIG. 12.—Fore and middle legs and tarsus of *Marellia remipes* (female).

A, right fore leg, posterior surface. B, right middle leg, posterior surface. C, apical portion of tibia, tarsus, and pretarsus of right middle leg, ventral view.

Ar, arolium; *Cx*, coxa; *Fm*, femur; *Pln*, planta; *Ptar*, pretarsus; *Tar*, tarsus; *Tb*, tibia; *TP*, tarsal pulvilli; *Tr*, trochanter; *Un*, claws; *Utr*, unguitractor plate.

flat. The lateral margins of the tibia bear the usual rows of spines, which, because of the flattened form of the tibial edge, appear like indentations rather than spines. In the last three interspinal spaces of the inner margin there is a fringe of stiff hairs (*C, h*) of which the function is unknown to the writer. Judging by the position of the shaft of the tibia, which in its distal dilated part may be distinguished only as a median thickening along the ventral surface, it seems that the outer margin is more expanded than the inner one.

At the tip of the tibia, there are four very strong, movable tibial spurs (fig. 13, *TSr*) which are curiously shaped like boats. Their upper surfaces are concave, excavated with raised margins, and their

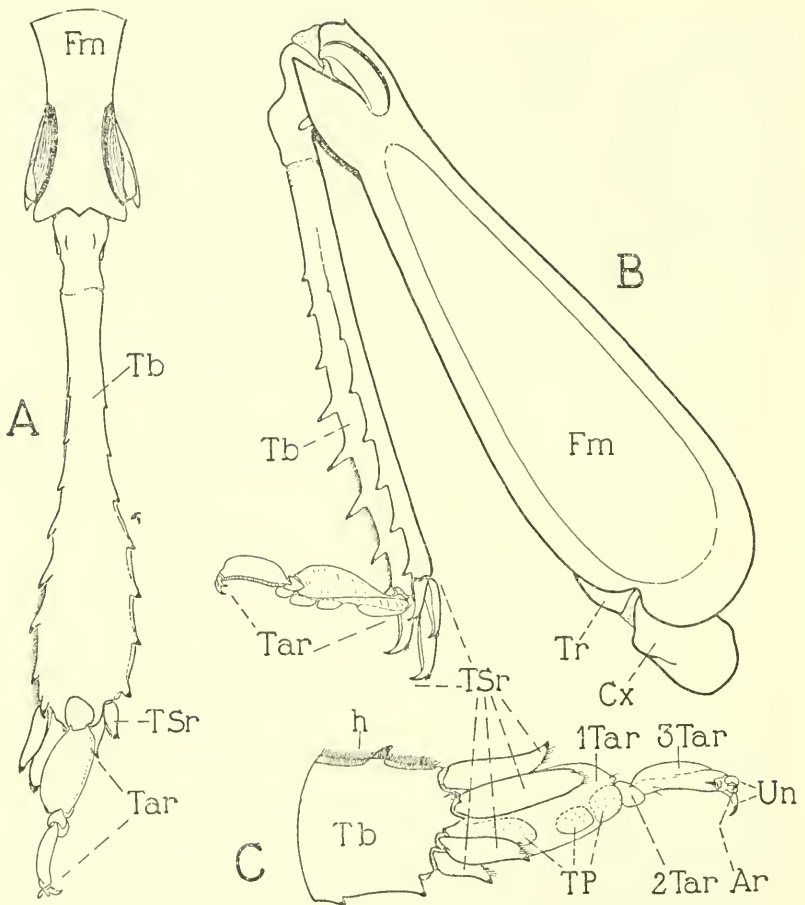


FIG. 13.—Hind leg of *Marellia remipes* (female).

A, right hind tibia and apical portion of femur, dorsal view. B, right hind leg, lateral (anterior) view. C, apical portion of right hind tibia and tarsus, ventral view.

Ar, arolium; *Cx*, coxa; *Fm*, femur; *h*, fringe of hairs in the inner margin of the apical portion of tibia; *Tar*, tarsus; *Tb*, tibia; *TP*, tarsal pulvilli; *Tr*, trochanter; *TSr*, tibial spurs; *Un*, claws.

ventral sides are strongly convex transversally. Each spur ends in an acute upwardly directed point, which bears a tuft of stiff bristles on its ventroposterior surface.

In the rearward stroke of the motion of swimming, the tibial spurs serve as supports for the dilated hind tarsi, keeping them from being bent down by the resistance of the water. The tarsi are freely mov-

able upward (see fig. 13 B) so that the spurs probably act to avoid slipping on the smooth surface of the leaves when the insect jumps from them.

An expanded distal portion of the hind tibiae is not an uncommon feature among semiaquatic orthopterans. It can be observed in the *Tetrigidae* and in other grasshoppers of semiaquatic habits, such as *Cornops aquaticum* (Covelo de Zolessi, 1956) and others. The hind tibiae of *Marellia remipes* seem, however, to be the most perfected swimming organs among the true acridoid grasshoppers, being supplemented in their function by the tarsi, as described immediately below.

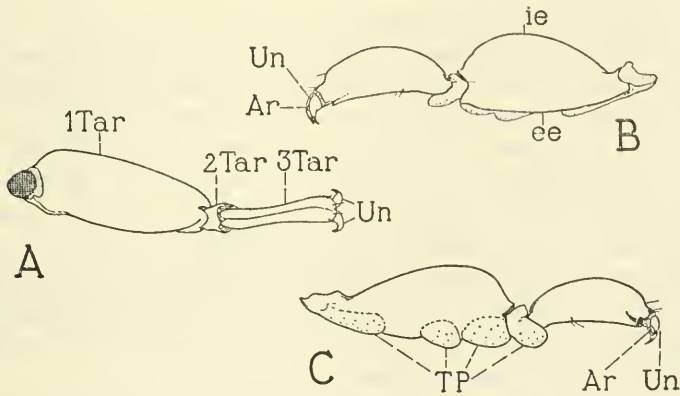


FIG. 14.—Tarsus of the right hind leg of *Marellia remipes*.

A, dorsal view. B, lateral (external or anterior) view. C, mesal (internal or posterior) view.

Ar, arolium; *ee*, external edge of first tarsomere; *ie*, internal edge of same; *1Tar*, *2Tar*, *3Tar*, first, second, and third tarsomeres; *TP*, tarsal pulvilli; *Un*, claws.

The hind tarsi.—The hind tarsus of *Marellia* (fig. 13, *Tar*, fig. 14) presents a striking form, being indeed highly modified in relation to the function of swimming. The first and third tarsomeres (fig. 14, *1Tar*, *3Tar*) are expanded and, when the tarsus is extended as for swimming, the tibial spurs support the first tarsomere from behind (see fig. 13 C).

The first tarsomere is the largest of the three. Its margins are expanded and upcurved, especially the inner one. The whole first tarsomere is affected by a helical torsion (Rosas-Costa, 1940), and from a nearly horizontal plane in its basal portion it turns inward to an almost vertical position in its distal part. The inferior surface of this

first tarsomere shows the usual three cushionlike tarsal pulvilli (figs. 13 C, 14 C, TP).

The second tarsomere (fig. 14 A, 2*Tar*) is as usual the smallest of the three, and the least modified. The third (3*Tar*) is large and compressed, showing a peculiar expansion of its upper margin. In its position it follows the torsion shown by the first, being in an almost vertical, slightly inclined plane, so that its external surface can be seen from above (see fig. 13 A). The pretarsus is similar to the pretarsi of the front and middle legs and shows likewise a poorly developed arolium.

VI. THE ABDOMEN

The abdomen of *Marellia remipes* is conical in shape (fig. 15), its apical portion being distinctly pointed. As we shall see later, the terminal structure of the abdomen in *Marellia* is markedly different from that of most grasshoppers, particularly in the females.

The whole abdomen is somewhat depressed in shape; the sternal region is broad and flat, and the terga show a distinct median dorsal carina from which the sides of this region slope down and out to meet the sterna. A transversal section of the abdomen is shaped like a triangle with a flat, broad base and convex sides. In the ovigerous female the contours of the abdomen become rounded. In the male the abdomen is more slender than in the female, and its subterminal part is slightly enlarged transversally.

In its pregenital or visceral part, the abdomen of *Marellia* does not show major differences from the corresponding region of *Dissosteira* (Snodgrass, 1935a), *Doclostaurus* (Jannone, 1939), or *Nomadacris* (Albrecht, 1956). It shows, however, differences of detail, especially in regard to the number and disposition of the spiracles.

The first abdominal spiracle (fig. 15, 1*Sp*) is remarkably large, much larger than the following ones. Below this spiracle, on the edge of the first abdominal tergum, there is a region covered with hairs which continues over the membranous zone below the tympanum and the posterior part of the edge of the first tergum to the whole inferior edge of the second tergum where the second abdominal spiracle (2*Sp*) is located. The first abdominal spiracle is covered by the pronounced lobe of the costal region of the fore wing already described. This circumstance, its large size, and the presence of what looks like a zone of hydrofugous hairs in its vicinity, suggest that this spiracle may play an important role in the respiration of the insect when submerged. The second abdominal spiracle (2*Sp*), surrounded by dense pilosity and protected by the ample base of the hind femur, may also

contribute to subaquatic breathing. We must recall here that the mesothoracic spiracle (fig. 8, Sp_2), covered by the posterior part of the lateral lobe of the pronotum, is also unusually large, and also has a hairy zone in its neighborhood. These characteristics lead us to think that the mechanism for subaquatic breathing comprises three pairs of spiracles—the mesothoracic and the first two abdominal ones—the three of them protected by adjoining structures and connected

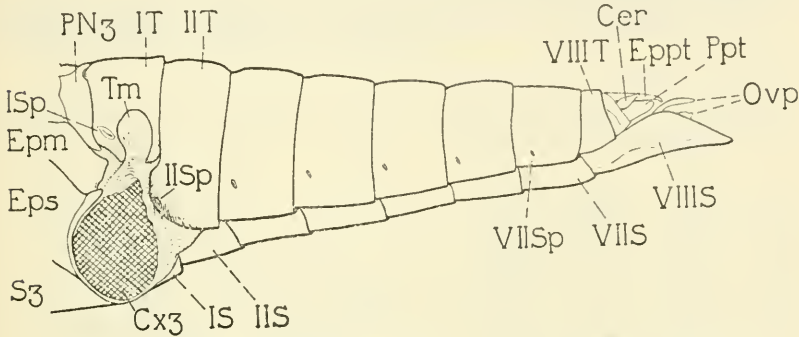


FIG. 15.—Abdomen and base of thorax of *Marellia remipes*, female.

Cer, cercus; *Cx₃*, coxal cavity of hind leg; *Epm*, epimeron; *Eppt*, epiproct; *Eps*, episternum; *Ovp*, ovipositor; *PN₃*, metathoracic postnotum; *Ppt*, paraproct; *S₃*, metathoracic sternum; *IS*, *IIS*, *VIIS*, first, second, and seventh abdominal sterna; *VIIIS*, eighth abdominal sternum, or genital plate of the female; *ISp*, *IISp*, *VIIISp*, first, second, and seventh abdominal spiracles; *IT*, *IIT*, *VIIIIT*, first, second, and eighth abdominal terga; *Tm*, tympanum.

with zones of hydrofugous hairs retaining air bubbles. Unfortunately the writer has not had on hand live specimens to prove these inferences at the time of making this study.

The rest of the abdominal spiracles (see fig. 15) are located rather high on the lateral parts of the tergal plates. An unusual detail of the female abdomen is the absence of spiracles on the eighth tergum, the last pair being on the seventh (*VIIISp*). The male abdomen, on the contrary, has a pair of spiracles on the eighth tergum (see fig. 19 A, *VIIIIT*). The lack of spiracles on the eighth tergum of the female abdomen is a curious fact for which the writer has not been able to find an explanation, unless it is related in some way to oviposition under water, to which we shall refer later in this paper.

The cerci (figs. 15, 16 B, 19 A, B, *Cer*) are similarly shaped in both sexes. They present a bulbous basal part which tapers to a bluntly pointed apex. In the male they are longer and slightly curved inward.

VII. THE OVIPOSITOR AND RELATED STRUCTURES

The terminal part of the female abdomen in the family Pauliniidae is very unusual, and the ovipositor differs considerably in several details from the usual acridoid ovipositor. The external aspect of this terminal part of the female abdomen has been described by Uvarov (1929) and Rosas-Costa (1940) for the species *remipes* and by Willemse (1948) for *M. clearei*.

The end of the female abdomen in *Marcellia remipes* (figs. 16, 17 A) is characterized by an extraordinarily enlarged eighth sternum

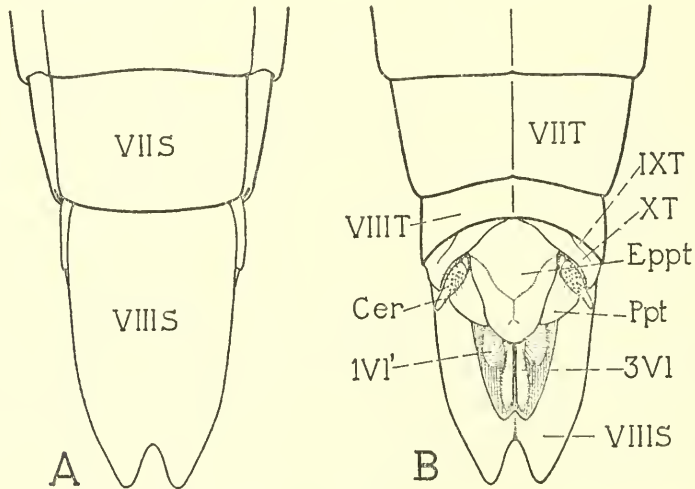


FIG. 16.—End of abdomen of *Marcellia remipes*, female.

A, ventral view. B, dorsal view.

Cer, cercus; *Eppt*, epiproct; *Ppt*, paraproct; *VIIS*, seventh abdominal sternum; *VIIIS*, eighth abdominal sternum, or subgenital plate of the female; *VIIIT*, *VIIIT*, seventh and eighth abdominal terga; *1VI'*, basal lobe of the first valvula of ovipositor; *3VI*, third valvulae of ovipositor.

(*VIIIS*) which constitutes a curiously shaped subgenital plate. This subgenital plate extends considerably beyond the tip of the ovipositor, which is practically lodged in a cavity on its dorsal surface and in such a way that only the tips of the first and third valvulae emerge from it. The present study has been made on alcohol-preserved specimens, but in the dried ones the ovipositor is often still more retracted, so that in a lateral view of the abdomen not even the tips of its valvulae show. The female subgenital plate can be properly called troughlike, as does Uvarov in his description of the genus (1929). The apex of this subgenital plate is flattened, decurved, and has a tri-

angular excision in its apical part (see fig. 16). Its whole upper surface, especially at the edges of the depression where the ovipositor is located, is densely covered by long, light-colored hairs. This pilosity again suggests a hydrofugous structure that may be related to oviposition. For the sake of clarity the hairs have been omitted in the illustrations.

The epiproct of the female (figs. 16 B, 17 A, *Eppt*) is roughly rhomboidal in shape and shows a distinct Y-shaped sulcus on its upper surface, with its branches diverging anteriorly. The paraprocts (*Ppt*) are slightly shorter than the epiproct.

The ovipositor.—The general structure of the ovipositor can be observed in figures 16 B and 17. The usual elements of the acridoid ovipositor can be easily recognized in it, but their shapes are here strongly modified.

The first or ventral valvulae (fig. 17 B, C, *1Vl*) are the strongest of the valvulae and constitute the most conspicuous part of the ovipositor. Their shape is most unusual: they present a basal, laterally expanded lobe (figs. 16 A, 17 B, *1Vl'*), and a distal, apical part (fig. 17, *1Vl*). The basal lobe is armed with a row of stiff bristles on its upper lateral margins, and it is the only part of the first valvulae that can be seen in a dorsal view (fig. 16, *1Vl''*). The apical parts of the first valvulae (fig. 17, *1Vl*) are narrow and have a linear series of stiff bristles directed upward and curved rearward on their dorsal surfaces (figured only in fig. 17 B). The external upper edges of the dorsal surface of these distal lobes and the external surface of their apices are distinctly denticulate. The basal, laterally expanded lobes of the first valvulae might represent the lateral basivalvular sclerites described by Snodgrass (1935a) in the first valvulae of the ovipositor of *Dissosteira*, but in order to ascertain this, a study of the muscles would be necessary. If they do represent the basivalvular sclerites, these sclerites are in *Marellia* united to the rest of the valvula in a continuously sclerotized structure.

The second valvulae (fig. 17 C, *2Vl*) are a pair of slender, pointed lobes arising between the bases of the first and third valvulae. They are similar in shape to those of *Dissosteira*.

The upper or third valvulae (figs. 16 B, 17, *3Vl*) are, like the first, of a most unusual shape. They are very long and slender, their apical portions decurved, with a somewhat excavated upper surface. Even from above (fig. 16 B, *3Vl*) the tips of these valvulae are somewhat expanded laterally or spatulate, and their edges and apices are distinctly granulated. In an upper view of the female abdomen, the tips of the third valvulae cover the apical lobes of the first ones which lie

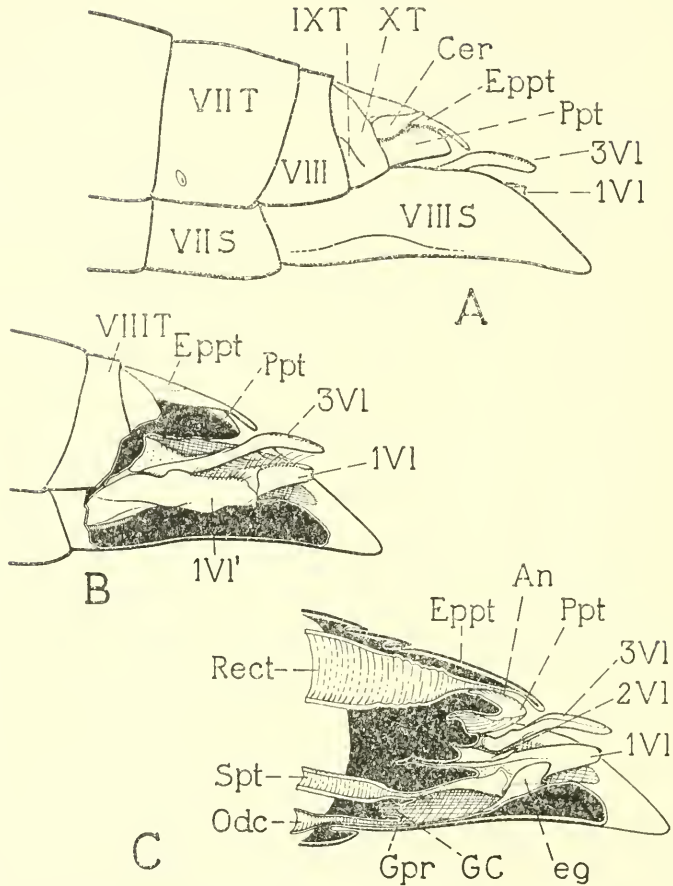


FIG. 17.—End of abdomen and ovipositor of *Marellia remipes*.

A, end of abdomen, lateral view. B, same, with left paraproct and cercus, part of eighth, ninth, and tenth terga, and part of subgenital plate removed to show ovipositor. Valvulae shown are those of the left side, external view. C, vertical section of end of abdomen (median plane). Valvulae shown are those of the right side, internal view.

An, anus; *Cer*, cercus; *eg*, egg guide; *Eppt*, epiproct; *GC*, genital chamber; *Gpr*, gonophore; *Odc*, oviduct; *Ppt*, paraproct; *Rect*, rectum; *VII S*, seventh abdominal sternum; *VIII S*, eighth abdominal sternum, or subgenital plate of the female; *Spt*, spermatheca; *VIII T*, *VIIIT*, *IX T*, *X T*, seventh, eighth, ninth, and tenth abdominal terga; *1VI*, *2VI*, *3VI*, first, second, and third valvulae of ovipositor; *1VI'*, basal lobe of first valvula of ovipositor.

directly underneath them. On their ventral surface, the third valvulae have a row of strong, long bristles that curve rearward (figured only in fig. 17 B).

These upper valves have been variously qualified as "feeble" (Uvarov, 1929) and "atrophic" (Rosas-Costa, 1940). They appear indeed feeble if compared with the strong upper valves of the usual acridoid ovipositor. When seen in its entire length (fig. 17 B, C *3Vl*), however, they are not suggestive of atrophy or disuse. They are indeed strongly modified in relation to an unusual mode of oviposition, but they look like perfectly functional organs.

On the floor of the depression of the subgenital plate that harbors the ovipositor, there is a well-developed egg guide (fig. 17 C, *eg*) which intervenes between the first valvulae.

The genital chamber (fig. 17 C, *GC*) is elongated and shows on its roof the opening of a large spermatheca (*Spt*), and the gonophore on the floor (*Gpr*).

VIII. THE EGG POD

The egg pods of *Marellia remipes* have been found and described by the writer (Carbonell, 1957). They represent perhaps the most unusual type of egg pod found in any grasshopper, on account of their shape and the fact that they are laid under water, adhering to the undersurface of the floating leaves of the host plant. Another very unusual type of acridoid egg pod has been recently described in Argentina (Rosas-Costa, 1950; Liebermann, 1951). It pertains to the grasshopper *Scotussa cliens* (Stal). As that of *Marellia*, the egg pod of *Scotussa* is epiphytic, being deposited by the insect on the upper surface of the leaves of umbelliferous plants of the genus *Eryngium*. But the egg pod of *Scotussa* is in every other respect entirely different from that of *Marellia*, being shaped like a mantid ootheca and is aerial instead of subaquatic.

The egg pod or ootheca of *Marellia remipes* (fig. 18) has the general shape of an inverted pyramid and adheres by its flat, basal upper surface to the underside of the floating leaves of the host plant. It is, hence, entirely submerged under water, and its only possible communication with the atmospheric air would be through the leaf itself, which has on its inferior face a layer of aerenchyma. The apical or inferior end of the egg pod has the form of a blunt, somewhat curved lobe (*h*).

The study of a considerable number of egg pods has shown that, though they are somewhat variable in size and shape, they have a remarkably uniform organization. They present invariably a slightly concave anterior or frontal surface with raised lateral edges, which

may be called the opercular surface (*Op*) on account of its opening in an operculum-like fashion (as shown in fig. 18 D) when the hoppers hatch. We will, then, call the side of the egg pod opposite the frontal or opercular surface *dorsal*, and its side walls *lateral*.

The lateral walls of the egg pod are transversally convex, and they

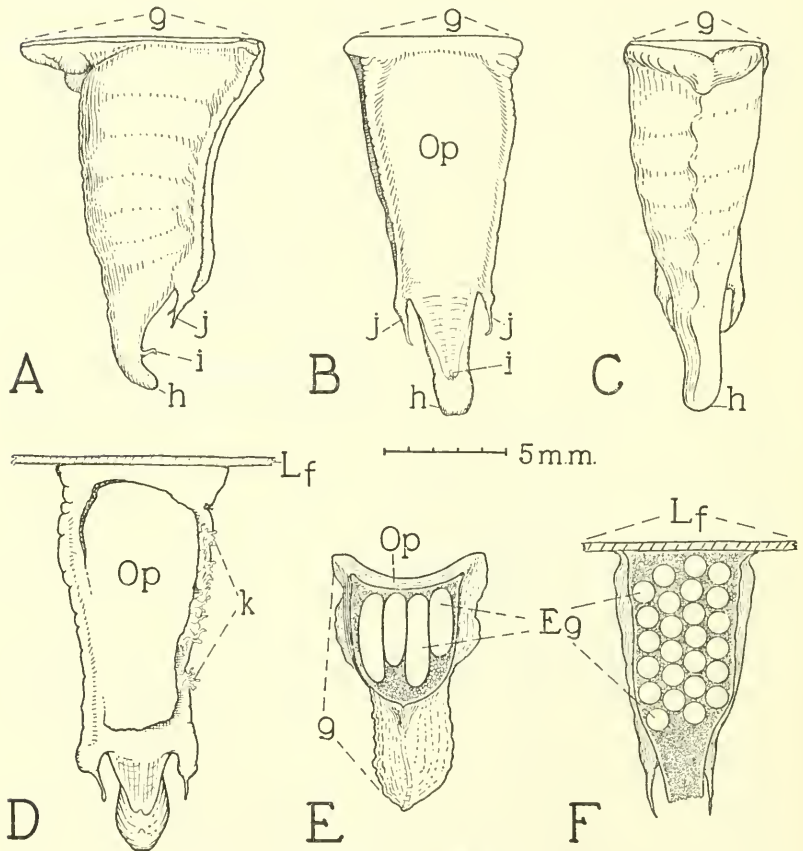


FIG. 18.—The egg pod of *Marellia remipes*.

A, lateral view. B, frontal or opercular view. C, posterior view. D, egg pod opened by the hatching of the hoppers, frontal or opercular view. E, horizontal section of egg pod. F, vertical section of egg pod, across the eggs. (After Carbonell, 1957.)

Eg, eggs; *g*, upper or basal surface of the egg pod, which adheres to the inferior surface of the leaves; *h*, apical or inferior lobe of the egg pod; *i*, median frontal process of the egg pod; *j*, *j*, lateral frontal process of the egg pod; *k*, cast skins of the intermediate moult left by hoppers after hatching; *Lf*, floating leaf of host plant; *Op*, opercular surface.

meet opposite the frontal surface to form the strongly arched dorsal wall, which shows a sinuous crest along its midline (see C).

The basal or upper surface of the egg pod (*g*) which adheres to the leaf (*Lf*) is always irregular in outline. It invariably shows a flat lobe that extends backward from the dorsal part of the ootheca (shown in fig. 18 A, E). The adherence of this basal surface to the leaf is remarkable, and when it is forcibly taken from the leaf it usually carries a piece of the leaf epidermis with it.

The inferior part of the frontal or opercular surface shows a peculiar disposition. There are on it two slender, lateral frontal processes (*A*, *B*, *j*, *j*) which prolong the raised lateral edges of the opercular surface, and a median small, upcurved process (*i*) on the frontal side of the apical lobe of the egg pod. The bases of these three processes limit a triangular, somewhat excavated area on the frontal surface of the apical lobe of the ootheca.

As can be observed by sectioning the egg pod (*E*, *F*), the eggs occupy only the upper or basal two-thirds of it. They are always arranged in four vertical rows, usually of six or seven eggs each, making on the average a total of 23 to 25 eggs. Occasionally an unusually large pod with a greater number of eggs can be found. The eggs are embedded in the usual hardened frothy secretion which completely envelops them. The apical or inferior third of the egg pod, which contains no eggs (*F*), is entirely formed of this hardened secretion.

Inside the egg pod, the eggs lie in a horizontal position. The cephalic end of the embryo is always directed toward the frontal or opercular surface. The egg pods are always located near the edges of the leaves, with the frontal or opercular surface directed outward, i.e., toward the edge of the leaf. As we shall see below, this fact must be related to the way in which the egg pod is laid.

Though the actual oviposition has not been witnessed by the writer, he has advanced a tentative explanation of the way in which it may be done (Carbonell, 1957). The anatomy of the female abdomen and the structure of the ovipositor have suggested to him the following mode of oviposition: the ovipositing female, sitting near the edge of the upper surface of a floating leaf, with her abdomen pointing outward, retrocedes and submerges its tip, reaching the inferior surface of a nearby leaf. Then the emission of the frothy cemental secretion begins, perhaps preceded by a scratching of the underside of the leaf by the upper valvulae of the ovipositor. After the preparation in this way of the flat foundation of the egg pod, its construction proceeds by

the actual laying of the eggs. The series of eggs would be deposited in this way from the upper part downward to the apex. After the eggs are laid, the emission of the frothy cemental secretion continues for a while, and the apical pointed lobe of the egg pod is built, its particular structure being shaped after the end of the female abdomen, the lateral frontal processes (*j, j*) corresponding to the cerci, and the front median process (*i*) being a mark left by the median excision of the subgenital plate.

If we observe the egg pod from its lateral surface (fig. 18 A), its whole form and pattern is suggestive of the described mode of oviposition. We must observe that according to this explanation, the abdomen would be at the beginning of the oviposition nearly horizontal and parallel to the leaf surface. As the oviposition proceeds, it would describe an arc by pivoting on its base, its distal part being at last at an angle with its first position. The somewhat arched shape of the egg pod and the fanlike pattern of its lateral walls support this explanation. The inclination of the frontal surface of its apical lobe, as seen from the side, would mark the final inclination of the female abdomen. We must remark, by the way, that this final position of the abdomen is the same as that shown by the usual ground-laying grasshoppers during oviposition. The following facts, in the writer's opinion, further support his explanation.

a. The location of the ovipositor in a cavity formed by a large subgenital plate makes its situation adequate for attaching the egg pod to the undersurface of the leaves when the insect is in the normal resting position and the abdomen horizontally extended.

b. The location of the egg pods, always near the edges of the leaves, and their orientation with the frontal or opercular surface toward the leaf edge, is also in favor of the said mode of egg laying. So is the position of the cephalic pole of the embryo, which in other grasshopper egg pods points to the side where the egg-laying female is during oviposition.

c. If we apply the end of the abdomen of a female of *Marellia* to the frontal area of the apical lobe of an egg pod in such a way that the upper surface of the subgenital plate lies against it, there can be observed a perfect coincidence of their different parts. The median frontal process of the apical lobe of the egg pod (fig. 18, *i*) fits into the terminal emargination of the subgenital plate (see fig. 16 B); the lateral frontal processes of the egg pod (fig. 18, *j, j*) closely embrace the abdominal end at the level of the cerci, and the excavated triangular area delimited by the bases of the three mentioned processes



The habitat of *Marcellia remipes* (near Cuareim River, northern Uruguay) : Floating leaves of the water poppy *Hydrocleis nymphoides*. Some of the leaves are partially eaten by the insects. (From Carbonell, 1957.)

on the terminal lobe of the egg pod exactly coincide with the triangle limited on the end of the female abdomen (fig. 16 B) by the bases of the cerci (*Cer*) and the anterior end of the excision of the subgenital plate. The mentioned triangular area on the frontal surface of the terminal lobe of the egg pod being somewhat excavated, it receives perfectly the slightly prominent epiproct and apices of the upper valvulae of the ovipositor.

Hatching was not observed by the writer, but on two occasions, a group of first instar hoppers was seen on the upper surface of a leaf, and the empty egg pod found on its underside. One of these empty egg pods is represented in figure 18 D, and it can be observed in it that the hatching of the hoppers partially detaches an operculum-like portion of the frontal surface (*Op*), and that the hatching hoppers, on emerging from under this operculum, leave the skins of the intermediate moult (*k*) trapped along its edge. Apparently the hoppers undergo this intermediate moult (embryonal moult of authors) when leaving the egg shell and either float to the surface and then swim to the leaf, or crawl on the egg pod and around the leaf to reach its upper side.

IX. THE MALE GENITALIA

The end of the male abdomen as seen from the outside (fig. 19) is not less peculiar than the corresponding region of the female. As has been already stated, the eighth abdominal tergum bears a pair of spiracles in the male, while these are lacking on the same segment of the female.

The most conspicuous feature of the terminal part of the male abdomen is the ninth sternum (fig. 19, *IXS*), modified in this species to form a large, undivided subgenital plate. There is no trace on the ninth sternum of the division into a proximal and a distal or apical part, shown by other grasshoppers. The whole of the subgenital plate of the male in *Marcellia* is conical in shape, ending in an elongated, blunt point.

Seen from above, the end of the male abdomen (fig. 19 B) shows the ninth and tenth terga (*IXT*, *XT*) deeply emarginated posteriorly. In this emargination the epiproct (*Eppt*) and the cerci (*Cer*) are located. The tenth tergum bears on its upper part a pair of small, lobiform, dark-colored furculae (*f*).

The epiproct (*Eppt*) is subtriangular and elongate. Its lateral margins show a dark-colored indentation a little beyond the middle of its length. The paraprocts (*Ppt*) slightly surpass the tip of the epi-

proct, and between their apices part of the membranous pallium (*Pal*) can be seen.

The cerci are similar in shape to those of the female, but they are a little longer and have their apices curved inward. The base of the male cercus has a small, dark-colored tubercle, with its apex directed toward the edge of the epiproct.

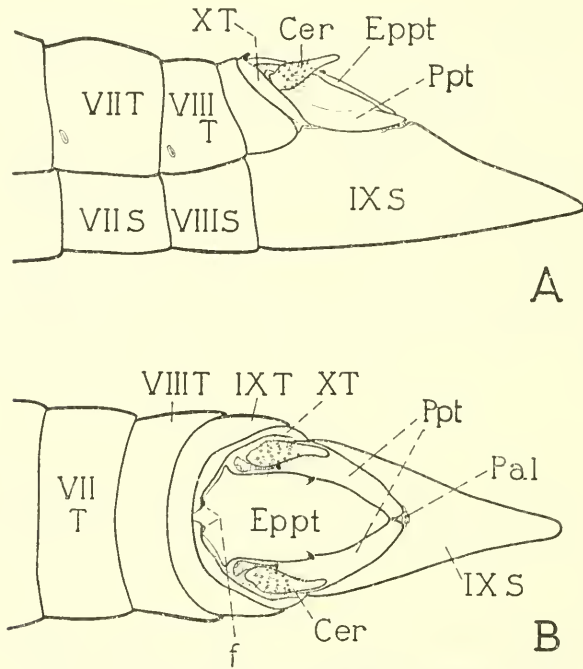


FIG. 19.—End of abdomen of *Marellia remipes*, male.

A, lateral view. B, dorsal view.

Cer, cercus; *Eppt*, epiproct; *f*, furcula; *Pal*, pallium; *Ppt*, paraproct; *VIIS*, *VIIIS*, seventh and eighth abdominal sterna; *IXS*, ninth abdominal sternum, or subgenital plate of the male; *VII T*, *VIIIT*, *IXT*, and *XT*, seventh, eighth, ninth, and tenth abdominal terga.

The phallic complex.—The general structure of the phallic organ in *Marellia remipes* and its relations to the terminal part of the male abdomen are shown in figure 20 A. The retracted phallus is bulblike and shows rather extended external sclerotizations. As can be seen in the figure, the whole of the phallic organ is enclosed within the greatly enlarged subgenital plate and covered by the hood of the pallium (*Pal*), the epiproct (*Eppt*), and the paraprocts (*Ppt*).

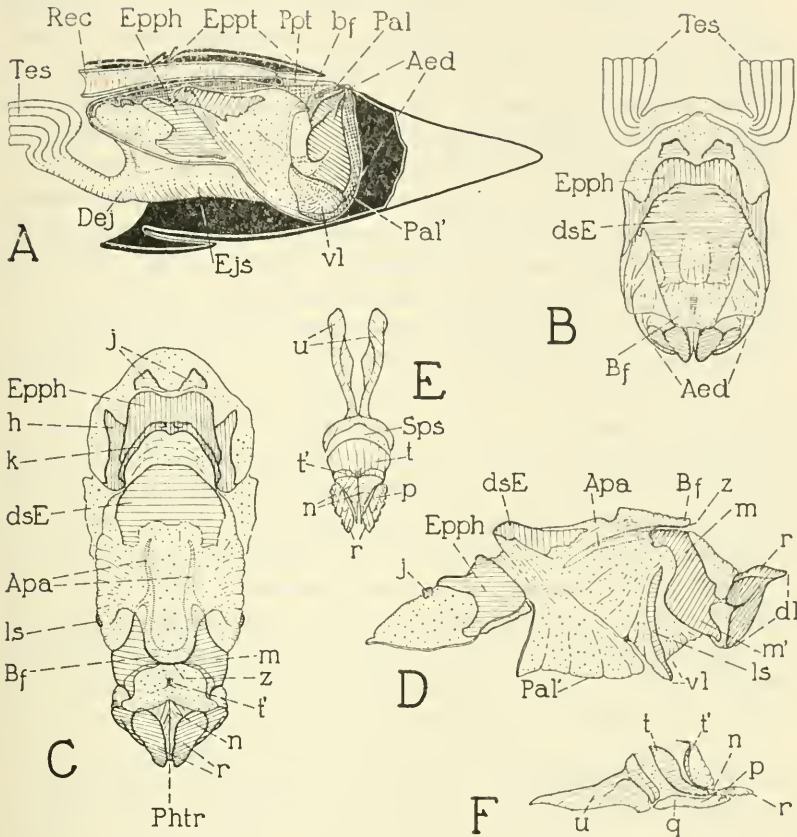


FIG. 20.—Male genitalia of *Marellia remipes*.

A, the phallic organs inside the end of the abdomen, lateral view (lateral wall of left side of abdomen removed). B, the phallic organs, retracted, dorsal view. C, same, extended, dorsal view. D, same, lateral view, from left side. E, endophallus, dorsal view. F, same, lateral view, from left side.

Aed, aedagus; *Apa*, apodemes of aedagus; *Bf*, basal fold; *Dej*, ejaculatory duct; *dl*, dorsal lobe of aedagus; *dsE*, dorsal sclerite of ectophallus; *Ejs*, ejaculatory sac; *Epph*, epiphallus; *Eppt*, epiproct; *h*, lateral lobe of epiphallus; *j*, anterior processes of epiphallus; *k*, posterior processes of epiphallus; *ls*, lateral sclerite of ventral lobe of aedagus; *m*, *m'*, proximal part of dorsal lobe of aedagus; *n*, anterior (dorsal) apical processes of aedagus; *p*, posterior (ventral) apical processes of aedagus; *Pal*, pallium; *Phtr*, phallotreme; *Ppt*, paraproct; *q*, posterior (ventral) lateral sclerite of phallotreme cleft; *r*, distal part of dorsal lobe of aedagus; *Sps*, spermatophore sac; *t*, bridge of anterior phallotreme sclerites; *t'*, posterior or external part of the bridge of anterior phallotreme sclerites; *tes*, testes; *u*, lateral plates of endophallus; *vl*, ventral lobe of aedagus; *z*, zygoxa of aedagal apodemes.

In the description of the phallic organ of *Marellia remipes* that follows and in the corresponding figures, the nomenclature of Snodgrass (1935a) has been used. In order to facilitate its comparison with the phallic complexes of other Acridoidea as described by Dirsh (1956), the nomenclature of that author is given in parentheses.

The phallic organ of *Marellia* protrudes from the floor of the genital chamber when in its retracted position (fig. 20 A). The membrane that forms this floor (ectophallic membrane) covers its basal part, being folded at its distal end in what is called the basal fold (*Bf*), under which emerges the apical part of the aedagus (*Aed*). On this membranous cover is the sclerite known as the epiphallus (*Epph*).

The epiphallus of *Marellia remipes* (fig. 20 A, B, C, D, *Epph*) is fairly similar in form to the same sclerite in the only other genus of the family, *Paulinia*, as described and figured by Radclyffe-Roberts (1941) and Dirsh (1956). It has rather large lateral lobes (lateral plates) (*h*) and a pair of anterior processes (ancorae) (*j*) that, unlike those of *Paulinia* which form a part of the epiphallus, are connected to it only by membrane. On the posterior part of the epiphallus, there is a pair of raised, crestlike posterior processes (lophi) (*k*) which extend along its posterior margin and nearly meet on the median line. No separate oval sclerites can be seen. These sclerites are present in *Paulinia*, and a study of the muscles of *Marellia* might reveal that they are incorporated in the lateral lobes of the epiphallus.

A peculiar feature of the floor of the genital chamber (ectophallic membrane) in *Marellia* is the presence of a large sclerite posterior to the epiphallus, which is here called the dorsal sclerite of the ectophallus (*dsE*). In the retracted phallic organ (fig. 20 A, B, *dsE*) it covers hoodlike the posterior processes of the epiphallus (lophi) (C, *k*). Its anterior margin is always definite, being molded on the shape of the posterior margin of the epiphallus, while its posterior margin weakens gradually into membrane, showing variable contours in different individuals. In order to extend the phallic organ, it is necessary to lift this sclerite to dislodge it from the epiphallus. Then it can be seen that it is separated from the epiphallus by a considerable stretch of membrane (see fig. 20 C, D, *dsE*).

The aedagus (A, B, *Aed*) is, as usual, divided into a ventral lobe (A, D, *vl*) and a dorsal lobe (D, *dl*). The ventral lobe is almost entirely membranous but shows two definitely sclerotized areas in the form of elongate, curved lateral sclerites (C, D, *ls*) along its lateral edges.

The dorsal lobe of the aedagus (*r*) appears to be formed in *Marellia* by the confluence of several parts which form two lateral halves of a

sheathlike hard covering of the terminal portion of the dorsal lobe. These lateral halves of the sheath appear to be formed by, or at least connected to, the lateral plates of the proximal part (m, m') (to which they are connected by sclerotized bridges shown in fig. 20 D), and to the posterior lateral sclerites of the phallotreme cleft (see below), which join the sheath at its upper apical part. The distal part of the dorsal lobe is, as usual, cleft by the phallotreme ($C, Phtr$).

The lateral sclerotized plates (m, m') of the proximal part of the dorsal lobe of the aedagus (rami of cingulum) are prolonged anteriorly by a pair of internal, rather weak parallel apodemes ($C, D, A\phi a$). The bases of the apodemes are united by a curved bridgelike zygoma (z) from which arises the membrane forming the basal fold (Bf).

The endophallus of *Marellia remipes* (E, F) is similar in several respects to that of *Paulinia* as described by Radclyffe-Roberts and Dirsh (loc. cit.) but presents some marked differences too. The dorsal or anterior sclerites of the phallotreme cleft and corresponding apical processes (valves of cingulum) (C, E, F, u) are small and membranous at their apical ends. They are united anteriorly by the bridge of the dorsal phallotreme sclerites (arch of cingulum) (t, t') which is double, having an anterior or internal part (t) covering the posterior wall of the spermatophore sac ($S\phi s$) and a posterior or external part (t') that continues in the membranous wall of the dorsal lobe of the aedagus at its dorsal part (see fig. 20 C, t').

The posterior or ventral sclerite of the phallotreme cleft (F, q) and corresponding posterior or ventral apical processes of the aedagus (apical valves of penis) (E, F, p) are continued externally into the distal part of the dorsal lobe of the aedagus (r) and the rest of the apical sheath of the dorsal lobe (sheath of penis).

The lateral plates of the endophallus or endophallic plates (basal valves of penis) (E, F, u) are united by a posterior cuplike bridge that covers the posterior wall of the spermatophore sac ($S\phi s$). The lateral plates are not expanded laterally as in *Paulinia*, nor do they show distinct gonophore processes as in this latter genus.

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THE FIRST LEG SEGMENTS IN THE CRUSTACEA MALACOSTRACA AND THE INSECTS

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INTRODUCTION

One of the great services Dr. R. E. Snodgrass has rendered to our science is to have pointed out in several of his recent works the lack of coherence still prevailing between the data of insect morphologists and those of specialists in other classes of Arthropoda. In his fine treatise of 1952 (pp. 284-285), for instance, he observes that one does not know what can correspond in the inferior classes of Arthropoda to those sclerites at the leg bases that we have studied so thoroughly in the Apterygota.

We preferred not to try to settle this question before acquiring a sufficient knowledge of the said formations in the Apterygota themselves. Their diversity within this subclass is so great that what they can have in common remained unknown for a long time. Hard work was needed to make up for this lack of knowledge and to enable us to show within the limb base new guiding marks in which we only now have taken interest, namely, the ties of the endosternites. These are more or less numerous according to the morphological types under examination; a great deal of experience was necessary to distinguish and recognize them in the various types.

As our attempts proved convincing, we set about gathering the elements of an answer to the question raised by our eminent American colleague. The Myriapoda¹ gave us little useful information; their supracoxal structures are too specialized. The Crustacea Malacostraca turned out to be of far greater interest in this connection, and we have already published a short paper² on them. We are pleased to offer in the present article, as a tribute to R. E. Snodgrass, more complete explanations and some illustrations on the same subject.

It is known that we have observed in quite varied types of Apterygota the presence of two main overlying supracoxal zones: the ana-

¹ *Scutigera*, *Lithobius*, *Cryptops*, *Scolopendra* (unpublished observations).

² Proc. 10th Internat. Congr. Ent., Montreal, 1956, vol. 1, pp. 489-490, 1958.

pleuron and the catapleuron. Furthermore, between the latter and the coxa, we have proved the presence of a trochantin certainly homologous with the trochantin of the Orthopteroidea (Carpentier, 1946, 1955), but this may be but a derivative of the coxa, in spite of the development and the individualization which it attains in certain orders.

Now, the question is, do all these formations exist in the Malacostraca as well, and if so, from what part of the leg do they start in a proximal direction?

To take a stand in this matter was to choose between two interpretations of the limb base which have been opposed to each other for a long time; one of them, advocated by Hansen (1893, 1925, 1930) and accepted by other writers including Vandel (1949), maintains that the insect coxa does not correspond morphologically to the coxopodite of the Crustacea but to the basipodite. Thus Hansen could homologize the coxal stylus of the Machilidae with an exopod. And on our part, we were tempted to see in the precoxopodite and coxopodite of the Crustacea the probable equivalents of the main supracoxal arcs of the Apterygota.³

However, the Crustacea Malacostraca compelled us to reject such homologizing. As we were trying to find to what part of the leg base the pleural region of the Apterygota corresponds, we had to acknowledge the accuracy of a former opinion, which regarded the coxa simply as homologous with the coxopodite; the correctness of this opinion will so be proved.

BASIPODITE AND COXOPODITE

Our researches on the Malacostraca concerned various species, particularly *Anaspides*⁴ and *Penaeus*. We first studied *Anaspides*, which is the "most primitive" genus of the subclass. The thoracic limbs of this malacostracan, mainly the maxilliped, have been considered by Hansen and other morphologists as having best preserved the organization of the primitive biramous limb. Neither Hansen⁵ nor Snodgrass,⁶ who has lately taken up the study of these appendages, saw an independent precoxopodite. According to those authors the precoxopodite of these "primitive" legs would be imbedded in the lateral

³ Lameere (1935, p. 70) regarded these homologies as "probable."

⁴ *Anaspides tasmaniae* Thoms., specimens of which were sent to us by Prof. E. Percival (Christchurch, New Zealand), thanks to the kind offices of our colleague Prof. H. Damas (Liège).

⁵ Hansen, 1925, pp. 102-103 and pl. 5, fig. 3e, f, h.

⁶ Snodgrass, 1952, p. 135, fig. C.

region of the thoracic segment in the shape of a rather reduced "laterotergal plate." It would be, after all, a "pleuron," the aspect of which would be quite different from that of a basal ring of the limb.

The only typical precoxopodite that Snodgrass observed in the arthropods in general is the "subcoxa" of *Strigamia*. This one completely encircles the coxa but remains a part of the body wall. *Strigamia* is a geophilomorphous chilopod, an arthropod the whole organization of which is far "less primitive" than *Anaspides*. Hence Snodgrass thinks (1952, p. 208) that, after all, there is no convincing evidence for a theory according to which a subcoxa, or primitive pleuron, would originally have made up the functional base of the limb of the arthropods.

However, we had to check whether the base of the maxilliped had been correctly described and figured. Snodgrass's data do not fit in very well with Hansen's (1925), and the results obtained by the latter have not been discussed. There is nothing astonishing in the fact that Snodgrass could not study with the same degree of care every detail which comes up in so vast and extensive a work as his. But here a greater accuracy is necessary.

We thought that the first point to check in *Anaspides* was to which segment of the limb the exopod is attached. Hansen regarded it as pertaining to a very short basipodite. Snodgrass, who neglected this last segment, saw the exopod attached, quite proximally, to the following segment, which is well developed and which Hansen named preischiopodite. We found that Snodgrass was right. Our figure 1c shows that the exopod mainly pertains to a differentiated region at the proximal end of the large segment of the leg. This "preischiopodite" is thus the true basipodite. Besides it is quite usual for the exopod of the thoracic limbs of the Malacostraca to pertain to the base of the basipodite.⁷ These relations are the same as those we observed in a general way in the Malacostraca we studied (see for instance *Penaeus*, fig. 2). The exopod of the thoracic legs of *Eupagurus* which puzzled Hansen (1925, p. 143) and which we reexamined with care is at least as proximal as that of *Anaspides*. Besides, the Danish writer found that one could be tempted to refer it to the coxopodite as well as to the following segment.

Yet the reduced region of the maxilliped as well as of the legs of *Anaspides*, which Hansen regarded as a basipodite, remains for us equivalent to a segment. This one is indeed very short, so short that on the side toward the body of the crustacean one could see but a

⁷ The "base" of a segment we define as its proximal end.

mere border line between two successive segments. However, the dissection shows that we have to do with a true segment and that this segment is a coxopodite. Despite the imperfect preservation of our material, we saw that a group of muscles inserted in the insects near the point where the trochantin articulates with the coxa, is inserted in *Anaspides* on our coxopodite and not on the base of the coxopodite of the other authors.

The reduced segment is, on the other hand, not merely a trochantin, a skeletal element which had never before been found in crustaceans but which we had some reason to look for in these arthropods. If we

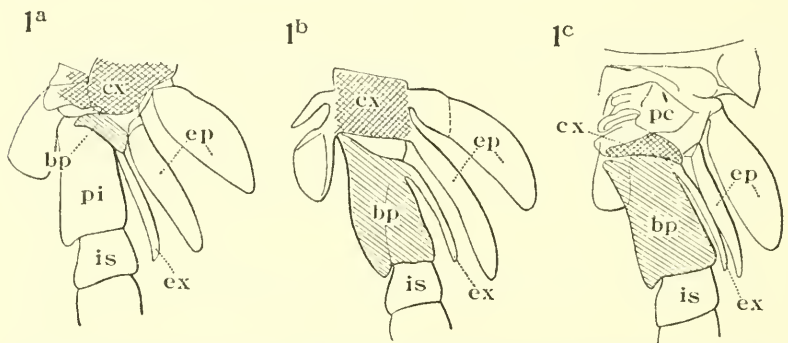


FIG. 1.—*a*, Basal part of the right maxilliped of *Anaspides tasmanicae* Thomson, posterior view, setae omitted. From Hansen, 1925. *b*, Idem. From Snodgrass, 1952. *c*, Idem. Original; new interpretation.

bp, basipodite; *cx*, coxopodite; *ep*, epipodite; *ex*, exopod; *is*, ischiopodite; *pi*, preischiopodite; *pc*, precoxopodite.

had to do only with a trochantin—the basipodite of Snodgrass and ours—it would be one that should possess at least some features of a coxa. But it actually resembles the insect trochanter by the extrinsic musculature which is inserted on its proximal end, opposite to the group of the levator and depressor muscles. In many insects the latter group contains muscles arising from the notum, the longest extrinsic muscles of the leg.⁸ *Anaspides*, however, had only rather short depressor muscles. Since we raised the question of the trochantin of crustaceans, let us point out that in the species of crustaceans where it is found best differentiated, it still presents the appearance of a part of the superior border of the coxa. This is to be recalled and examined thoroughly when it comes to investigating the origin of the trochantin.

⁸ See *Lepismachilis* (Barlet, 1946, fig. 2, TR-NT); but the said muscle does not exist except in the anterior leg of the machilid.

The "trochanteral" characteristics of the basipodite are particularly clear-cut in the Penaeids (figs. 2 and 4), primitive decapods. In each of the thoracic legs of a *Penaeus*⁹ the proximal end of the basipodite forms with the preceding segment a typically trochantero-coxal articulation; this end of the basipodite is obliquely cut and bears two tendons. These tendons are opposite each other, and one of them bears a depressor muscle arising from the notal region. There is another similarity with the insects (fig. 4): beneath the tendon of the depressor muscle, a muscle (*bp-ca*) is attached on the wall of the basipodite of *Penaeus*; it runs along the ischiopodite and the meropodite to be eventually inserted on the proximal extremity of the carpopodite,¹⁰ which is known to be homologous with the insect tibia. A similar tibio-trochanteral muscle can be found in the insects, *Periplaneta*¹¹ for instance. The facts we have just mentioned fit in with a homologization of the basipodite with the trochanter, a conception which, as we saw, has already been accepted by a number of authors but which it was useful to buttress with further arguments.¹²

PLEURAL CHARACTERISTICS OF THE PRECOXOPODITE

Thus the so-called coxopodite of *Anaspides* is actually a free precoxopodite, and this precoxopodite must correspond to the pleuron or to a part of the insect pleuron. Now let us see whether the malacostracan precoxopodite actually shows, especially on the inner side, at least some of the characteristics of a pleuron. We shall check, this time beginning with *Penaeus*, the precoxopodite of which, like an insect pleuron, has become a part of the lateral wall of the thoracic segments. We know¹³ how this may have happened. The cylindrical

⁹ *Penaeus caramote* Risso of the Mediterranean.

¹⁰ Hinton (1956, p. 11) wrongly denies the existence of this muscle in Crustacea.

¹¹ Original observation. Carbonell (1947) does not figure this muscle.

¹² Then the stylus on the coxa of the Machilidae cannot be homologous with an exopod. Besides it is attached rather distally on the posterior side of the coxa. This stylus is probably homologous with the epipodite which we see on the external side of the coxopodite of the penaeids and other Malacostraca.

¹³ See Snodgrass, 1952, p. 146, fig. 41 D. The imbedding of the proximal segment of the leg of the decapods in the thoracic lateral wall has long since been accepted (Calman, 1909; Hansen, 1893) after observations of Claus (1885) on the shift of the pleurogills and arthrogills of *Penaeus* toward the end of the embryonic life. Yet Heegaard (1947, p. 192) made certain reservations about those observations of Claus although he never wanted to reject them completely. Let us remark that elsewhere Heegaard (op. cit., p. 188) sees only two segments in the sympod of the penaeids.

segment of the leg, drawing back into the lateral wall, shortened to such an extent that it almost disappeared, except on the side where it has formed, up to a certain level, the mesal wall of the gill chamber of the decapod.

Our figure 2 shows the internal side of this wall above the third right pereopod of *Penaeus*.¹⁴ From the direction of the lines which margin or run across the precoxopodian wall, we have the impression that it penetrated into the lateral wall like a wedge, pressing back the primitive wall more toward the middle of the segment than at the ends. Therefore, at these two extremities, the old wall could remain rather close to the coxa.¹⁵ The coxa itself has grown like a wedge toward the lateral wall at its anterior angle (α) which is elevated compared with its posterior angle (β); a third angle (γ) exists on its proximal side; the upper frame of the coxa is thus triangular. The proximal side of the coxa is dihedral in keeping with a certain overlapping of the leg bases; it has an oblique anterior side against which the back of the coxa of the preceding leg can be moved and a posterior side which runs along the margin of the sternite.¹⁶

At each angle α and β of the coxa there is an articulation with the pleuron; it is a kind of "suspension" of the coxa which really resembles that of the last two pairs of coxae of the Machilidae (Carpentier, 1946, fig. 6). It is one more reason why we consider the Machilidae as having preserved certain resemblances with the Crustacea.

Above the articulation of the angle α an apodeme (ap), which we have every reason to homologize with the pleural apodeme of the insects, arises and bends backward in *Penaeus* as well as in the last two thoracic segments of the Machilidae. The apodeme does not present any process in *Penaeus*, but we find a rudimentary one in *Amalopenaeus*.¹⁷ The apodeme divides the pleuron into two regions, anterior and posterior, which include the equivalents of the episternum and of the epimeron of the Pterygota. However, these regions are

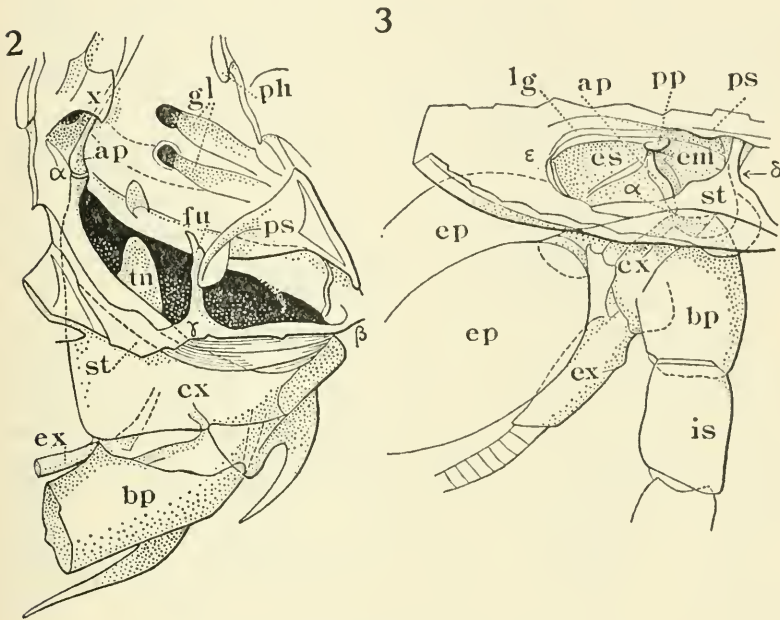
¹⁴ We have chosen this third leg as typical; it is far from the head and it is the last one of those which, even at their base, are not influenced by the specialization of the genital region.

¹⁵ This is only a general impression. We shall not be able to go into the details of the specialization which has affected the leg base, especially on the proximal side. Here we only suggest a few guiding marks.

¹⁶ Compare with the transversal sections of the coxae of a *Cambarus* on fig. 43 A of Snodgrass (1952).

¹⁷ *Amalopenaeus valens* S. I. Smith (we used some of the well-preserved specimens which had been brought back years ago by Prof. D. Damas from his expedition with the *Armauer Hansen*, 1922).

very unequal and their upper limits are indistinct. The region anterior to the apodeme appears to have very little extension, but its lower precoxal part obviously proceeds proximally to the anterior angle of the coxa. Higher, the same anterior region of the lateral wall bears a winding ridge of a general direction parallel to that of the pleural apodeme. This ridge, which is about abreast of the intersegmental



FIGS. 2 and 3.

Fig. 2.—Basal part of the 3d right pereiopod of *Penaeus caramote* Risso, seen from inside, setae omitted.

Fig. 3.—Basal part of 5th right thoracic limb (4th pereiopod) of *Anaspides tasmaniae* Thomson, seen from the front, setae omitted.

an, laterotergite, sclerite pertaining to a region which seems homologous with the anapleuron of the Apterygota; *ap*, pleural apodeme; *bp*, basipodite; *cx*, coxopodite; *e*, spot where the endosternal arm *e* is attached; *em*, epimeral region; *es*, episternal region; *ex*, exopod; *f*, spot where the endosternal arm *f* is attached; *fu*, furcal apophysis; *gl*, gill; *h*, spot where the endosternal tie *h* is attached; *is*, ischiopodite; *lg*, laterotergite; *ph*, phragm; *pp*, (medio)pleural process; *ps*, postpleural process; *st*, sternum; *tn*, trochantinal tendon; *x*, ax-shaped undetermined process.

a, antero-external angle and (*idem*) articulation of the coxopodite; *b*, postero-internal angle and (*idem*) articulation of the coxopodite; *γ*, internal angle; *δ*, internal articulation of the laterotergite; *ε*, external articulation of the laterotergite.

phragm (*ph*), has given birth to an ax-shaped process *x* for which there is no equivalent among the insects. A branchial shaft (*gl*) is attached externally to the base of the process.

The region of the lateral wall posterior to the pleural apodeme is very large.¹⁸ It bears externally two branchial shafts (*gl*); internally, in the back part of the segment, we find a strong infolding of the cuticle in the shape of a large triangular blade with a small terminal spatula. We call this large blade the postpleural process (*ps*). Does it proceed from the wall of the precoxopodite or does it pertain to the primitive lateral body wall, which locally is not pressed back? We cannot answer this question at the present time.

Near the proximal angle (γ) of the coxal margin a furcal apophysis (*fu*) arises. It takes its rise at the edge of the sternal plate, at the limit between this sternal plate and the membranous strip, the only remnant, proximally, of the precoxal wall. This spot corresponds to the spot which was pointed out by Weber (1928, p. 250) as typical of every furcal apophysis of the Pterygota.¹⁹

We have figured and described the postpleural process and the furcal apophysis of *Penaeus* as separated from each other, as they will be found after a specimen is treated with caustic potash. Without this treatment, these two internal formations of the cuticle would have appeared wrapped in a common subhypodermal sheath²⁰ pertaining to an endoskeletal scaffolding (fig. 4) which we shall analyze further on. In *Cambarus*, an American crayfish, Snodgrass (1952, p. 156) saw likewise a "pleural apodeme" united with a "sternal apodeme" by certain "interlocking fimbriations"; these parts become disconnected, he explains, if the preparation is left to dry.

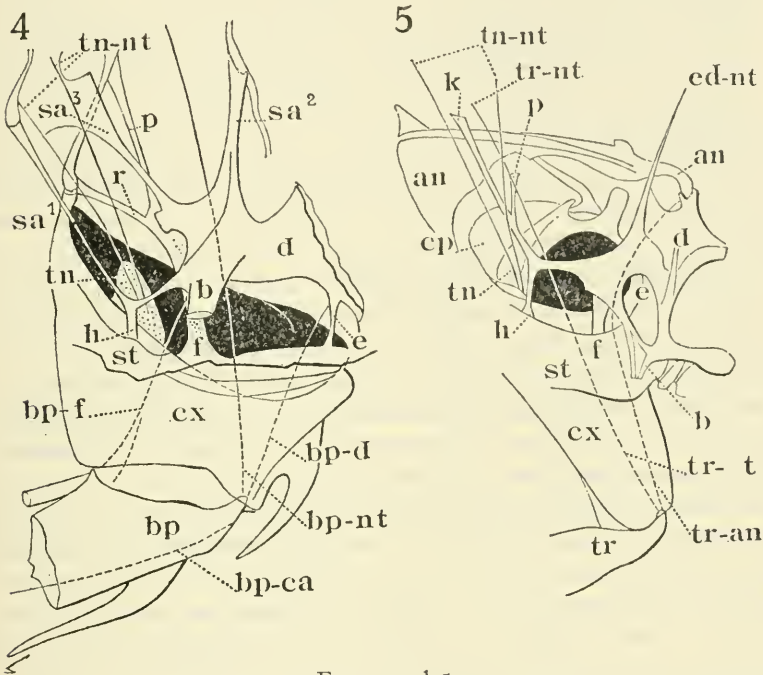
We know that the schemes of the thorax depicted in general treatises

¹⁸ In going over the series of precoxopodites of *Penaeus*, we come across some of them in which the two regions of the lateral wall are less unequal.

¹⁹ In a note written to do justice to all that may be valuable in Ferris's ideas, one of us (Carpentier, 1947, pp. 300-301) has maintained that in the insects, this one can pertain more to the proximal zone of the catapleural ring than to the sternum itself. Rendering an account of this note, Weber (1952, p. 110) unfortunately wrote that the basisternite is regarded in that note as a secondary formation. This is not correct.

²⁰ Let us keep in mind that we give this name to every endoskeletal scaffolding directly prolonging inward the basement membrane of the hypoderm. Muscles inserted on such an endoskeleton may be, of course, homologous with muscles inserted on cuticular infoldings encompassed with the hypoderm and thus with the basement membrane of the hypoderm (see Carpentier, 1946, pp. 171-172), whatever the chemical nature—not yet elucidated—of the subhypodermal formations.

on entomology do not show the furcal apophysis connected with a postpleural process but rather with the process of the (medio)pleural apodeme. However, the coexistence of the two kinds of processes has been observed in such insects as *Sialis* (Weber, 1928, fig. 14^b; Czihak, 1953, fig. 7) and in Lepidoptera (Weber, 1928, figs. 1^a



FIGS. 4 and 5.

FIG. 4.—Basal region of the 3d right thoracic limb of *Penaeus caramote* Risso, setae omitted.

FIG. 5.—Basal region of the prothoracic limb of a machilid. (Figure based especially on *Petrobius*.)

The two figures show the internal side, with the endosternite and some particularly interesting muscles (drawn with a single line).

an, anapleuron or anapleural pleurite; *ap*, pleural apodeme; *bp-ca*, muscle going to the carpopodite, homologous with a tibiatiochanter muscle in the insects; *bp-d*, other depressor of the basipodite; *bp-f*, levator muscle of the basipodite, homologous with a trochantero-furcal muscle of the insects; *bp-nt*, depressor of the basipodite, homologous with a trochantero-notal (epimeral) muscle in the insects; *cp*, catapleuron; *cx*, coxopodite or coxa; *d*, *e*, *f*, *h*, *k*, *p*, arms of the endosternite homologized in the Apterygota; *ed-nt*, endosterno-notal muscle; *sa*, superior arms (not homologized in the Apterygota); *st*, sternite; *tn*, trochantin or its tendon; *tn-nt*, trochantino-notal muscles; *tr*, trochanter; *tr-an*, trochantero-anapleural muscle; *tr-nt*, trochantero-notal muscle.

and 9^a). The processes can be connected by muscular fibers or can be closely united. If the postpleuro-furcal complex has become somewhat voluminous, that with the (medio)pleural process can be found reduced or even lacking entirely. When we consider only the pterygotan insects, we might think that of the two ways in which the furca is united, that with the back is the more recent one. The Apterygota in which this way of union (fig. 5) is so widespread,²¹ the Myriapoda²² as well as the Crustacea, lead us to adopt the opposite opinion.

We have now to describe and to compare with what we have just seen the internal side of a precoxopodite of *Anaspides*. We shall use the fourth pereopod (fig. 3), that is to say, the antepenultimate leg as in the previous species. The precoxopodite of this leg being free and uncovered, since *Anaspides* does not have a carapace, it is quite different from the preceding one in its orientation and in its shape. It is not imbedded in the side of the thoracic segment and keeps a certain mobility by means of two articulations (ϵ , δ) with a particular sclerite of the lateral wall (*an*). Hansen (1930) took this sclerite for a part of the precoxopodite; Snodgrass (1952) named it laterotergite (*lg*). The posterior articulation (δ), the only one seen by those authors, has been interpreted by them as representing β of our figure 2 (*Penaeus*). We see at once on figure 3 that there is no pleural apodeme on top of it but that this apodeme (*ap*) is actually a part of the wall of the so-called coxopodite of the authors. The curved pleural apodeme (*ap*) bears at the top of the precoxopodite a process (*pp*) which may be the pleural process; but, considering its position in comparison with that of the process of the penaeids, we cannot yet give a definite answer. The precoxal wall is divided into an episternal region (*es*) and an epimeral region (*em*) of about the same surface area. The episternum is barred almost horizontally with an apodeme which joins *ap* at the top. Two large blades, or epipodites, are attached externally on the episternal region of *Anaspides*, while in the same region we saw but a single epipodian gill in *Penaeus*. Finally the furcal apophysis of *Penaeus* is completely wanting in *Anaspides*. The thoracic lateral wall of the latter crustacean is thus rather different from that of the first one; but the comparative study of the endoskeletal scaffoldings

²¹ The subhypodermal endoskeleton is united with it, or connected by a tie (the postcoxal tie *d*) at the back of the anapleural arc. See Carpentier, 1946, figs. 4 and 5 (prothorax of the Machilidae), and fig. 2 (*Ctenolepisma*); Barlet, 1951, fig. 1 (*Lepisma*), Carpentier and Barlet, 1951, fig. 2 (*Campodea*); unpublished (*Japyx*).

²² Unpublished observation.

and of their relations with the skin fortunately gives us better precision.

ENDOSTERNITES OF PENAEUS AND ANASPIDES

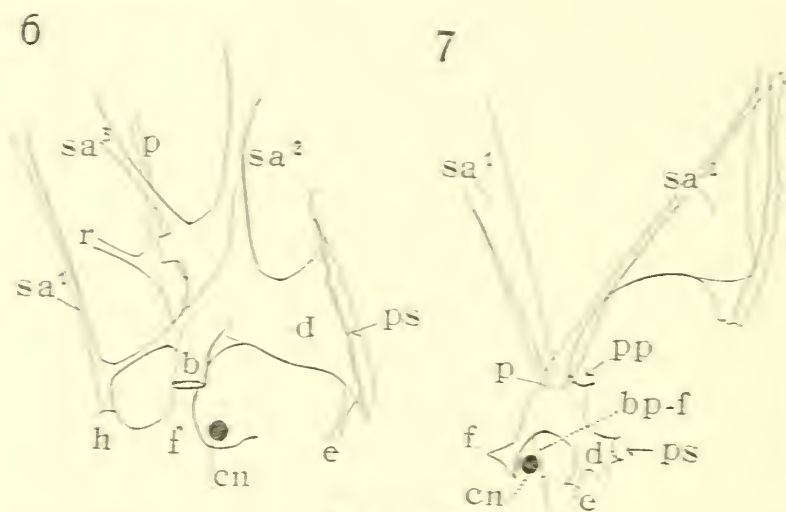
We have seen that the postpleural and furcal formations of the cuticle of *Penaeus* are wrapped in a common subhypodermal endosternal sheath. This endosternite (fig. 6) is unified, that is to say the right and left parts of the scaffolding are medially united by a transverse strip (*b*) going over the nerve cord. Such were the endosternites studied in the Lepismatidae, in the prothorax and mesothorax of the Machilidae, etc. On each side of the body, the endosternite is connected with the skin by ties. There are three superior arms (*sa*); we do not name them with more accuracy because we have not found their homologues—at least their endoskeletal homologues—in the insects. The first arm (*sa*¹) is very thin and could be confused with the pleural “tigelle” *k* of the Apterygota²³; but dorsally, instead of being connected with the notum, it is attached to the anterior phragm (fig. 2, *ph*). The upper arm (*sa*²) is attached to the posterior phragm; it is double and each of its branches toward the phragm is enlarged into a blade serving as a support to longitudinal muscles. The arms *sa*¹ and *sa*² could respectively correspond to the oblique muscles 75 and 77 (prothorax of *Lepisma*, Barlet, 1951, fig. 1); *sa*² could also correspond to 85 (mesothorax, idem) and 92 (metathorax, idem). This is one possibility.²⁴ A third and last superior arm (*sa*³) pertains to the lateral process (fig. 2, *x*), the morphological value of which we do not know.

All the other arms of *Penaeus* have been homologized and are designated therefore, on figure 6, by letters taken over from the notation system which was formerly adopted for the Apterygota. For instance the arm *p*, the identity of which is obvious; this arm connects the central part, *g*, of the endosternite with the pleural apodeme. The union is direct since there is no pleural process; in *Amalopenaeus* the union is achieved by means of a pleural process. Another lateral arm (*r*) pertains distally to the border between the precoxopodite and the coxa.

²³ See Carpentier, 1946, fig. 2 (*Ctenolepisma*), fig. 5 (*Petrobius*); Carpentier, 1949, fig. 5 (*Tomocerus*); Barlet, 1951, fig. 1 (*Lepisma*).

²⁴ Back in 1927, Cannon (p. 413) examined in a phyllopod crustacean the muscularization of endoskeletal elements. See also Manton, 1928. Without knowing anything about these results, we came to conceive the substitution of “tigelles” for muscles (Barlet, 1946, p. 182; Carpentier, 1949, p. 46, note 7; Carpentier and Barlet, 1951, p. 4). Chadwick (1957) exploited this idea about the Pterygota.

Its homologue was seen in a collembolan, *Tomocerus* (Carpentier, 1949, fig. 3). A last lateral arm (*d*) corresponds to the postcoxal tie of the Apterygota, but here it is quite voluminous for it contains the postpleural process (fig. 2, *ps*) in a cavity which extends a little into the transverse strip *b*.



FIGS. 6 and 7.

FIG. 6.—Endosternite of the 3rd thoracic segment (3d pereopod) of *Penaeus* sp. (off the Brazilian coast), right half seen from inside. The transverse strip *b* has been cut.

FIG. 7.—Endosternite of the 3rd thoracic segment of *Anargyris ramosior* Thomson, right part seen from inside.

b, *d*, *e*, *f*, *g*, *h*, *p*, *r*, arms homologized with those of the Apterygota, *bp-f*, levator muscle of the basipodite, homologous with *bp-f* of *Penaeus* (fig. 6) and with a trochantero-furcal muscle of the insects but missing in the Machilidae; *cn*, cranial nerve; *pp*, pleural process; *ps*, postpleural process; *sa*, superior arms non-homologized in the Apterygota; *sa*¹ could correspond to the muscle *sd-w* of the machilids [see fig. 3].

Finally, the endosternite is provided with three lower arms. Anteriorly we see *h* which proceeds in *sa*² and contributes toward making this one similar to *h* of the Machilidae. Toward the middle lies *f* which contains the furcal apophysis (fig. 2, *fa*) in a separate pouch, a little more distal than that of the spatula of the postpleural apophysis. Posteriorly we find the lower arm *e*; it presents with *d* similar relationships to the ones we studied in the Lepismatidae.²²

²² Carpentier, 1946, fig. 2. The postcoxal tie of the Lepismatidae is thin and does not contain a cuticular process. In *Petrobia* (op. cit., figs. 3 and 6) *e* has

On the whole we see thus that the equivalents of the majority of the endosternal arms of the Apterygota and particularly those which had appeared the most consistent and typical, have been found in *Penaeus*. The importance of this result is obvious.

We have now to describe the subhypodermal scaffolding of *Anaspides* (fig. 7). In spite of the great differences which it displays at first sight from that of *Penaeus* and in spite of its relative simplicity, it furnishes us on many points valuable information for the interpretation of the cuticular skeleton to which it pertains. In *Anaspides*, the endoskeleton is not unified; no strip *b* connects the right formation with the left formation. Each of them contains two superior blade-shaped arms, one (sa^1) pertaining to the front of the tergal region, the other (sa^2) arising from the back of the same region and in the proximity of which it is particularly wide. The two arms do not pertain to phragms but to "pseudophragms" (subhypodermal).

There are two lateral arms, and these are the most interesting. One of them (*p*) connects the endosternite with what we have interpreted as the process of the pleural apodeme (*pp*). This arm is interesting, first because it confirms our interpretation, then because of its shape: it is a sheath of the process, a sheath of the same type as (although smaller than) the "fourreau" which fits the long pleural horn of the Machilidae (Carpentier, 1946, fig. 6, and 1949, fig. 1). The other lateral arm (*d*), no shorter than the preceding one, is attached to what was supposed to correspond to a postpleural process (*ps*). Our supposition becomes thus a certainty.

If we really have to do with a postpleural process, it becomes obvious that this formation does not pertain to the precoxopodite but to the upper sclerite, the laterotergite. It seems to us that this sclerite, already present in *Anaspides*, must represent the anapleural region of the Apterygota. In keeping with this opinion, we have to discuss the following facts: In *Penaeus* (fig. 4) and other Malacostraca we have found a muscle (*bs-ps*) of the basipodite (trochanter) coming from the under part of the postpleural process. In the Machilidae we have recently found out that in the prothorax (fig. 5) a few fibers (*tr-an*), very close to those of the depressor of the trochanter (Barlet, 1946, fig. 2, TR-ED), come from a sclerite (*ibid.*, *sp*) to which the

not been correctly located. Our researches after 1946 have shown that instead of "*f + e*" we should have written "*f*," and instead of "*i + d*" we should have written "*e + d*."

region *d* of the endosternite adheres and which must be anapleural.²⁶ There are two inferior arms of the endosternite of *Anaspides*: *f* and *e*. The arm *f* thus exists, but no furcal apophysis developed within it. Our figures 6 and 7 show that in *Anaspides* as well as in *Penaeus* the crural nerve *cn* passes between *f* and *e*. One will at once object that in the Apterygota the crural nerve is not posterior to *f* but anterior. This difficulty at first embarrassed us, but later we found that the crural nerve can be connected with the ganglion by two roots, one anterior to *f* (or *fu*), the other posterior. The two roots coexist in *Amalopenacus*, but quite often only the posterior root exists in the Crustacea. In the insects it seems that it is always the anterior one.²⁷ Thus our difficulty was only apparent.

We see that in spite of the difference of aspect and of composition of the endosternites of *Anaspides* and of *Penaeus* we have been led to locate in both crustaceans the homologues of the main lateral and inferior arms of the Apterygota.

CONCLUSIONS CONCERNING THE LEG BASE AND THE PLEURON OF THE MALACOSTRACA

We have presented in this paper a comparative analysis of these parts of the body only in two Malacostraca: that regarded as the most "primitive" of all and a decapod particularly "primitive" too. We have made a few references to other species which have also been studied. Our present knowledge of the Malacostraca may seem insufficient, but one should bear in mind that our study has dealt with only a very limited region of the body of the Crustacea and that this same region had been previously studied for many years with the greatest care and with exactly the same method on various Apterygota and even (unpublished) on Myriapoda. The experience so acquired will have kept us, let us hope, from making identifications based upon coincidences rather than upon a real morphological kinship.

At any rate one result of our researches seems to be beyond all question: the true pleural region of a malacostracon cannot contain

²⁶ In the first of our works on the Apterygota (Carpentier, 1946, p. 177) we indicated that this sclerite is "very ambiguous," but we thought that we could refer it to the catapleuron. The preoccupation to classify the propleural sclerites of the Machilidae according to two circles led to this interpretation, which seemed to be supported by certain features of *Thermobia* (Lepismatidae). However, it must be false as we found out later in our studies.

²⁷ Constant, too, in the Pterygota. One would not think so upon examining fig. 2 in Jösting's work (1942) concerning *Tenebrio*; but we were able to show that his figure is in error.

a segment of the leg more distal than the precoxopodite. What we have found by carefully examining the exterior of the leg has been confirmed—we think, in a conclusive manner—by the inspection of the interior of the precoxopodite. Whether this segment has remained free or has been imbedded in the thorax, it has displayed in both cases features which correspond with those of an insect pleuron. It has displayed the most typical relationships with the ventral endoskeleton previously found in the Apterygota. *Anaspides* most resembles the latter by the predominance of its subhypodermal endoskeleton, whereas *Penaeus*, by the development of its cuticular infoldings, is more like a pterygote.

The precoxopodite is thus morphologically equivalent to a unilaterally developed pleuron; but is it the entire pleuron? Most likely not, for the precoxopodite does not directly articulate on the tergum of the thoracic segment but on a “laterotergal” plate. This laterotergite bears posteriorly a process which the comparison with the insects led us to call postpleural. The laterotergal plate seems to pertain to a region homologous with the anapleuron of the Apterygota.²⁸ On the proximal side we never saw it achieve a complete circle, but in these arthropods, the anapleuron, in certain points, remains difficult to analyze.

According to these new data, what must we think of the “subcoxal theory”? Of course it is beyond doubt that the originally basal ring of the leg has secondarily been imbedded in the thoracic wall, but this ring may very well have produced only a part of the pleuron.

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²⁸ A priori, we can hardly accept the idea of the distinction of an “anapleuron” and of a “catapleuron” (precoxopodite) starting with the Crustacea. Indeed in the nauplius of various Crustacea, the segments of the sympod appear distinctly only some time after the hatching (Heegaard, 1947); but for the phylogenist what does this order mean according to which morphological details appear in a larva such as a nauplius?

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SPINASTERNAL MUSCULATURE IN CERTAIN INSECT ORDERS

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PART I. THE SPINASTERNAL MUSCLES OF THY- SANURA AND PTERYGOTE INSECTS

Within the muscular system of hexapods, the spinasternal muscles form a group which, though probably diverse in origin and development, is relatively easy to distinguish and define. The spinasternal muscles are widely distributed among modern species, and while they are not overly numerous, their number has evidently been altered greatly during the differentiation of the various orders. Thus, a comparative study should readily provide some notion both of the ancestral status of the spinasternal muscles and of their principal evolutionary trends.

As will be seen, muscles that belong to the spinasternal category have been found in one or another insect by many workers, yet few have recognized in them an evolutionarily significant element of the hexapod muscular pattern. I believe that these muscles are best understood as relics of a part of the early arthropod musculature that the insects are gradually abandoning. Reasons for this conclusion will be set forth in the sections that follow, for one must reach a clear decision on this point before one can apply data now available on the spinasternal muscles successfully to phylogenetic problems. My primary purpose here is therefore to review the distribution of the several spinasternal muscles throughout the class of insects, insofar as present information will permit.

Included among the muscles to be examined are all thoracic muscles with either or both attachments on the spinae or on their present morphological equivalents. The spinae (*sps*) are median intersegmental interneural apophyses, invaginated from the ventral integument. In some Apterygota they are found in the cervical, thoracic, and abdominal intersegments (Maki, 1938; Barlet, 1951, 1953, 1954), but they occur only in the first and second thoracic intersegmental regions of pterygote insects, except in *Grylloblatta*, which is reported (Walker

1938) to have a third spina, and possibly also in Mallophaga (Mayer, 1954). The spinal apophysis intrudes between the nerve cords from a sclerotized area of variable extent, the spinasternite, which in the thorax may be distinct from or fused to a greater or less degree with the preceding or succeeding segmental sclerite. Many Pterygota now have two such spinae, others one, and some none; in all these insects, the abdominal counterparts of the thoracic spinasternites are said to be included in the antecostae of the definitive abdominal sterna (Snodgrass, 1929). The former cervical spina of most insects has evidently been incorporated into the head, or even wholly lost; but its fate apparently varies in different species and has not been thoroughly studied.

In this paper, all spinasternal muscles are regarded as intersegmental, since they have at least one of their attachments on what is considered the morphological equivalent of a primary intersegmental groove. For similarly practical reasons, I shall refer here to all attachments of muscles on the furcal arms as segmental, although I have previously (Chadwick, 1957) argued that at least some of the furcal attachment sites are morphologically intersegmental.

SOURCES AND TREATMENT OF DATA

The literature now provides adequate though sometimes imperfect descriptions of thoracic structure for representatives of the Thysanura and 24 pterygote orders. I have checked or supplemented many of these observations by gross dissection of the same or closely related species, and assume responsibility for any interpretations or statements of fact in this paper that are not credited specifically to others. I must also bear the burden of all mistakes. Apart from my own failures and possible errors by the original authors, the necessity, for comparison, of translating into a single idiom the varied designations used by different writers for the several muscles has opened the way for misunderstandings on my part. Besides, there are instances where different workers disagree as to the facts, and there are others where the homologies of the parts that bear the muscles are unclear, or even in dispute. Fortunately, only a small fraction of the data is subject to uncertainty from these causes and, though some future corrections of detail are to be expected, they should have little impact on the general import of the observations.

There is still need for descriptive study in some areas. Among the Apterygota, it is only for *Lepisma* (Barlet, 1951, 1953, 1954) that we have sufficiently accurate detailed descriptions of both skeleton and

musculature, although helpful information on this and other thysanurans is given in the reports of Maki (1938), Argilas (1941), Barlet (1946, 1948, 1949, 1950), Carpentier (1946), Chaudonneret (1950), and Carpentier and Barlet (1951), among others; and for Collembola by Denis (1928), Maki (1938), and Carpentier (1947, 1949). Maki (1938) also describes a dipluran, *Lepidocampa*, but leaves one in doubt as to essential skeletal details; and there seems likewise to have been no suitable study of a proturan. Data useful for our present purpose are also lacking for the following Pterygota: Diploglossata, Zoraptera, Anopleura, Strepsiptera, Raphidioidea, and Siphonaptera; and knowledge of some of the other winged orders is at present restricted to the adult form of a single species. From the point of view of the present study, there has been no adequately extended investigation of the embryogeny of any insect, though it is apparent that certain questions as to structural homologies will be answerable only in the light of such information.

Our analysis will therefore be confined largely to the Thysanura and the 24 pterygote orders for which reasonably complete and accurate observations are available, with only occasional allusions to reports on other insects. When these missing groups, particularly among the Apteriygota, can be included, the number of known spinasternal muscles will certainly be increased to some extent. However, the general pattern of these muscles emerges quite clearly from the data already at hand.

Since it is not proposed to describe the complete spinasternal musculature order by order, the following summary of the sources selected for this study may be helpful. Unless otherwise noted, the works cited concern adult insects.

THYSANURA. Maki, 1938 (*Lepisma*, *Pedctontus*); Barlet, 1951, 1953, 1954 (*Lepisma*).

COLLEMBOLA. Maki, 1938 (*Neanura*, *Folsomia*).

BLATTARIAE. Carbonell, 1947 (*Periplaneta*); Chadwick, 1957 (19 spp., nymphs and adults, ventral intersegmental muscles only).

COLEOPTERA. Bauer, 1910 (*Dytiscus*); Speyer, 1922 (*Dytiscus* larva); Murray and Tieggs, 1935 (*Calandra*, larva and adult); Maki, 1938 (7 spp.); Jöosting, 1942 (*Tenebrio* larva); Chadwick, unpublished (*Cybister* larva).

DERMAPTERA. Maki, 1938 (*Anisolabis*, *Labia*); Chadwick, unpublished (*Forficula*).

DIPTERA. Samtleben, 1929 (culicid larvae); Mihalyi, 1935 (*Musca*); Maki, 1938 (5 spp.); Williams and Williams, 1943 (*Drosophila repleta*); Zalokar, 1947 (*D. melanogaster*); Bonhag, 1949 (*Tabanus*); Miller, 1950 (*D. melanogaster*).

EMBIODEA. Verhoeff, 1904 (*Embia*); Maki, 1938 (*Oligotoma*).

- EPHEMEROPTERA. Dürken, 1907 (mainly *Centroptilium* and *Ephemercella*, nymphs and adults); Knox, 1935 (*Hexagenia*, nymph and adult); Maki, 1938 (*Ecdyonurus*).
- GRYLLOBLATTODEA. Walker, 1938, 1943 (*Grylloblatta*).
- HEMIPTERA. Maloeuf, 1933 (*Nezara*); Maki, 1938, (*Eurostus*, *Sigara*); Rawat, 1939 (*Naucoris*); Larsén, 1945b, 1945c (numerous spp.); Griffith, 1945 (*Rhamphocorixa*); Qadri and Abdul-Aziz, 1950 (*Pyrilla*).
- HOMOPTERA. Berlese, 1909 (*Cicada*); Weber, 1928 (*Aphis fabae*); Maki, 1938 (*Huechys*, *Cicadella*, *Macrohomotana*); Mäkel, 1942 (*Pseudococcus*, immature and adult); Larsén, 1945c (*Cyclochila*); Roberti, 1946 (*Aphis doralis frangulae*).
- HYMENOPTERA. Nelson, 1925 (*Apis* larva); Weber, 1926 (*Vespa*), 1927 (*Schizocerus*, *Tenthredo*); Maki, 1938 (*Entomostethus*, *Philopsyche*, *Vespa*); Duncan, 1939 (*Vespula*); Snodgrass, 1942 (*Apis*).
- ISOPTERA. Fuller, C., 1924 (*Termes* et al.); Maki, 1938 (*Odontotermes*); Chadwick, 1957 (*Zootermopsis*, ventral intersegmental muscles only); Chadwick, unpublished (*Mastotermes*).
- LEPIDOPTERA. Forbes, 1914 (various larvae); Maki, 1938 (5 spp.); Chadwick, unpublished thesis (numerous species); Nüesch, 1953, 1954 (*Telea*).
- MALLOPHAGA. Mayer, 1954 (4 spp.).
- MANTODEA. Maki, 1938 (*Hierodula*); Levereault, 1938 (*Stagmomantis*); La Greca and Raucci, 1949 (*Mantis*); Chadwick, 1957 (*Tenodera* nymph, ventral intersegmental muscles only); Chadwick, unpublished (*Stagmomantis* nymph, ventral intersegmental muscles only).
- MECOPTERA. Maki, 1938 (*Neopanorpa*); Hasken, 1939 (*Panorpa communis*); Fuller, H., 1954, 1955 (*Borcus*); Chadwick, unpublished (*P. canadensis* and *P. submaculosus*).
- MEGALOPTERA. Maki, 1936 (*Chauliodes*); Czihak, 1953 (*Sialis flavilatera*); Kelsey, 1954, 1957 (*Corydalis*, larva and adult); Chadwick, unpublished (*Sialis* spp., *Corydalis*, larva and adult).
- NEUROPTERA. Korn, 1943 (*Myrmeleon*, larva and adult); Larsén, 1948 (*Chrysopa*); Czihak, 1956 (*Myrmeleon*, *Ascalaphus*, *Palparens*); Chadwick, unpublished (unidentified sp.).
- ODONATA. Maloeuf, 1935 (*Anax*, *Plathemis*, nymph and adult; Maki, 1938 (*Crocothemis*, *Psolodesmus*); Clark, 1940 (13 spp., nymph and adult); Grandi, 1947 (wing base).
- ORTHOPTERA. Voss, 1904-1905 (*Gryllus domesticus*); 1912 (*G. domesticus*, late embryo and nymph); DuPorte, 1920 (*G. assimilis*); Carpentier, 1921a (*Gryllotalpa vulgaris*); 1921b (*Tachycines asynamorus*); 1923 (*Curtilla*); Ford, 1923 (numerous spp., abdomen); Snodgrass, 1929 (*Dissosteira*); Camerlengo, 1936 (*Gryllotalpa*); Carpentier, 1936 (*Gryllotalpa*); Maki, 1938 (4 spp.); La Greca, 1939 (*Gryllotalpa*); Jannone, 1939 (*Doclostaurus*); La Greca, 1947 (various spp., wing articulations); 1948 (Acrididae, innervation of wing and wing muscles); Albrecht, 1953 (*Locusta*).
- PHASMATODEA. Jeziorski, 1918 (*Dixippus*); Maki, 1935 (*Megacrania*); Chadwick, unpublished (*Diapheromera*); cf. Marquardt, 1939 (*Dixippus*, innervation of muscles).
- PLECOPTERA. Wu, 1923 (*Nemoura*); Helson, 1935 (*Stenoperla*); Maki, 1938 (*Neoperla*); Grandi, 1948 (*Perla*); Wittig, 1955 (*Perla*, nymph and adult); Chadwick, unpublished (*Pteronarcys*, nymph and adult).

PSICOPTERA. Badonnel, 1934 (*Stenopsocus*); Maki, 1938 (*Psocus*).

RAPHIDOIDEA. Czihak, unpublished thesis (*Raphidia*).

THYSANOPTERA. Maki, 1938 (*Machatothrips*).

TRICHOPTERA. Maki, 1938 (*Stenopsyche*).

Throughout arthropod phylogeny, various muscles are subject to replacement by endoskeletal parts; and numerous examples of this typical trend are to be found among the spinasternal muscles of insects. The process has taken a variety of pathways, which this is not the place to discuss; the point of interest here is that the existence of such endoskeletal structures permits one in favorable instances to infer the place originally occupied by a muscle in some ancestor of the form under investigation. In the course of the present review, I have noted for certain species that endoskeletal structures, including ligaments, are the present equivalents of spinasternal muscles in others: attention is called to these examples in the discussion of the individual muscle types.

To designate the individual muscles, or their equivalents, I have used the topographical system adopted earlier (Chadwick, 1957); this method has its defects, but only some such scheme is applicable in the present context, and I have found none that is definitely superior. Each muscle recognized as a morphological entity is identified by a symbol that is formed by hyphenating the accepted abbreviations for the skeletal parts between which the muscle is stretched. The abbreviations are for the most part those given currency by Snodgrass (1929, etc.). Numerical subscripts, arabic for the thorax and roman for the abdomen, indicate the proper segmental affinity of an attachment. Correspondingly, intersegmental attachment sites are preceded by the appropriate numeral, beginning with 0 for the cervical intersegment; however, the customary designations *1cv*, *2cv* . . . for the cervical sclerites and *1ax*, *2ax* . . . for the axillary sclerites, the latter with segmental subscripts, are retained. A glossary of the abbreviations used follows in table I.

THE SPINASTERNAL MUSCLES

The place of the spinasternal muscles in the general muscular pattern of insects invites further study, for which we must look principally to the comparative embryologists of the future. Here one can only indicate the nature of the problem.

In addition to the characteristic outer circular and inner longitudinal layers into which the bulk of the somatic musculature of hexapods and related animals can be resolved, a third class of muscles is repre-

sented by a series of transverse or oblique bands whose attachments on the body wall are commonly intersegmental. Some writers have regarded such muscles as offshoots of the outer circular layer, though other views are also tenable. Certain it is that the spinasternal muscles are related in part to this third category, whatever its source, for they share with it not only position in relation to attachment sites but the equally distinguishing feature of passing across the body internal to the principal nerve trunks. However, the definitive spinasternal musculature is too diverse to be derived solely from such an origin, and yet many of its components do not fit easily into either of the other recognized categories.

Posteriorly, the spinasternal muscles appear to be continuous with the ventral diaphragm, a fenestrated muscular and membraneous partition whose attachments on the anterolateral regions of the abdominal sterna are related morphologically to those of the thoracic transverse intersegmental muscles, but in some insects the ventral diaphragm itself extends into the thorax (Czihak, 1956), with attachments on what I have called the intersegmental laterosternites (*ils*) (Chadwick, 1957).

According to Roonwal (1937), however, the ventral diaphragm is formed in the embryo of *Locusta* from segmental mesoderm and is topographically dorsal to the transverse intersegmental muscles, which arise from the blood cell lamellae. Nevertheless, the muscular attachments of the ventral diaphragm to the "third spina" of some cockroaches and other pterygote insects are ventral to those of the other spinasternal muscles, whereas the transverse bands, where they occur, are usually the most dorsal of all elements inserted on the spina (see figures in Chadwick, 1957). Such apparent inconsistencies emphasize the need for further careful study of the genesis of the several muscular categories and of specific definitive muscles in a variety of insects and related forms.

The midventral attachments of the transverse muscles of insects on the interneural spinae may be secondary, although Wells (1944) has described in an annelid, *Arenicola*, transverse (oblique) muscles that originate dorsolaterally from the outer circular layer and form ventral connections with the connective tissue sheath of the nerve cord. In other worms and arthropods, the transverse muscles, when present, often pass from one side to the other without interruption, or are inserted centrally into a complex endoskeletal plate that is suspended in the body cavity between the nerve cords and the gut. The "oblique dorsoventral muscles" of Onychophora resemble those of *Arenicola*

in their dorsolateral origins, but the corresponding bands from opposite sides are inserted separately on the ventral body wall at loci that are mesad of the here widely divergent nerve cords (Sedgwick, 1888; Snodgrass, 1938). According to the scanty embryological evidence on insects, the transverse muscles in the embryos of Dermaptera and Blattariae (Heymons, 1895) arise as single bands that cross the body at each intersegmental fold (cf. Roonwal, 1937, cited above). During later embryonic development, the abdominal representatives are lost, and the thoracic transverse muscles acquire the typical connections with the spinae. This sequence of events is not universal, since Santleben (1929) has described both abdominal and thoracic transverse muscles in culicid larvae; while Ford (1923) and Maki (1938) record the persistence of transverse abdominal muscles in the adults of a number of pterygote insects. Such muscles are particularly well developed in the first abdominal intersegment of certain cockroaches (Chadwick, 1957). Czihak (1956) notes the presence of a transverse cervical muscle in the adult of *Myrmeleon*. From the descriptions of Thysanura and Collembola given by Carpentier and Barlet in references already cited, one judges that the transverse muscles of these apterygotes have largely given way to ligamentous derivatives that participate in the formation of the complex endosternum characteristic of these insects. The endosternum here commonly has per intersegment one or more median ventral attachments, also of a ligamentous consistency, that appear comparable with the spinal structures of pterygote insects. The abdominal endosterna of *Lepisma* are somewhat simpler than their thoracic counterparts, but are otherwise very similar (Barlet, 1954).

Although a postmetathoracic spina is not found in most Pterygota, the former general existence of such a structure is indicated not only by its presence in certain apterygotes (Maki, 1938; Barlet, 1951, 1953, 1954), in the Grylloblattodea (Walker, 1938, 1943), and possibly in Mallophaga (Mayer, 1954), but also by the muscular relationships in other primitive winged insects, in which the postmetathoracic homologues of the more anterior spinasternal muscles have a common mid-ventral junction that lies above the nerve cords but is without connection with the integument (Badonnel, 1934; Chadwick, 1957; Kelsey, 1957).

PRESENTATION OF DATA

It has been impractical to prepare tables that would collate the designations of all the original authors with those adopted in this study. Accordingly, I list in table 1 the principal spinasternal muscles together

with the orders from which they have been reported. Most of the significant variations that have been noted are mentioned in the discussions of muscle types that follow the table. Further details will have to be sought in the original sources, which have been tabulated by order in the list on pages 119-121.

TABLE I.—*List of thoracic spinasternal muscles and their distribution*

(Details will be found in the original references on pages 119-121 and under the discussion of muscle types in the text. In the table, *l* stands for larva, *n* for nymph, and *a* for adult, in instances where both the mature and immature forms have been found comparable yet different.)

<i>1sps-iils</i>	Thysanura; Blattariae; Coleoptera, <i>l</i> ; Dermaptera; Isoptera; Mantodea; Megaloptera, <i>l, a</i> ; Neuroptera, <i>l, a</i> ; Odonata, <i>n, a</i> ; Plecoptera, <i>n, a</i> ; Psocoptera; Trichoptera.
<i>1sps-cps₁</i>	Thysanura; Blattariae; Grylloblattodea; Homoptera; Isoptera; Mantodea; Megaloptera, <i>a</i> ; Orthoptera.
<i>1sps-fu₁</i>	Thysanura; Blattariae; Coleoptera, <i>l</i> ; Dermaptera; Embiodea; Grylloblattodea; Hemiptera; Homoptera; Hymenoptera; Isoptera; Lepidoptera; Mallophaga; Mecoptera; Megaloptera, <i>l</i> ; Odonata, <i>a</i> ; Orthoptera; Phasmatodea; Plecoptera, <i>n, a</i> ; Psocoptera; Trichoptera.
<i>1sps-fu₂</i>	Thysanura; Blattariae; Coleoptera, <i>l, a</i> ; Embiodea; Grylloblattodea; Hemiptera; Homoptera; Isoptera; Lepidoptera; Mantodea; Mecoptera; Megaloptera, <i>l, a</i> ; Neuroptera, <i>a</i> ; Orthoptera; Plecoptera, <i>n, a</i> ; Psocoptera; Thysanoptera; Trichoptera.
<i>1sps-2ils</i>	Thysanura; Coleoptera, <i>l</i> ; Dermaptera; Neuroptera, <i>l</i> .
<i>1sps-cx₁</i>	Thysanura; Blattariae; Coleoptera, <i>l</i> ; Hymenoptera; Isoptera; Lepidoptera; Megaloptera, <i>l, a</i> ; Neuroptera, <i>l, a</i> ; Orthoptera; Plecoptera, <i>n, a</i> ; Psocoptera; Thysanoptera; Trichoptera.
<i>1sps-cx₂</i>	Thysanura; Blattariae; Coleoptera, <i>l</i> ; Dermaptera; Grylloblattodea; Isoptera; Mallophaga; Megaloptera, <i>l</i> ; Orthoptera; Plecoptera, <i>n, a</i> ; Psocoptera.
<i>1sps-2sps</i>	Thysanura; Blattariae; Mantodea; Orthoptera; Psocoptera.
<i>2sps-2ils</i>	Thysanura; Blattariae; Coleoptera, <i>l</i> ; Dermaptera; Mecoptera; Megaloptera, <i>l, a</i> ; Neuroptera, <i>a</i> ; Odonata, <i>n, a</i> ; Orthoptera; Plecoptera, <i>a</i> .
<i>2sps-cps₁</i>	Blattariae; Grylloblattodea; Isoptera; Mantodea; Neuroptera, <i>a</i> ; Psocoptera.
<i>2sps-fu₂</i>	Thysanura; Dermaptera; Ephemeroptera; Hymenoptera; Mallophaga; Mecoptera; Neuroptera, <i>a</i> ; Odonata, <i>a</i> ; Orthoptera; Phasmatodea; Psocoptera.
<i>2sps-fu₃</i>	Thysanura; Blattariae; Coleoptera, <i>l, a</i> ; Dermaptera; Embiodea; Grylloblattodea; Hymenoptera; Isoptera; Mantodea; Megaloptera, <i>l, a</i> ; Neuroptera, <i>l</i> ; Orthoptera; Plecoptera, <i>n, a</i> ; Psocoptera.
<i>2sps-3ils</i>	Thysanura; Coleoptera, <i>l</i> ; Grylloblattodea ?; Megaloptera, <i>l</i> ; Odonata, <i>n, a</i> .
<i>2sps-iils</i>	Blattariae; Grylloblattodea (prob.); Megaloptera, <i>a</i> .

(Continued)

TABLE I.—(Continued)

<i>2sps-fu₁</i>	Thysanura; Blattariae; Dermaptera; Embiodea; Grylloblattodea; Isoptera; Megaloptera, <i>l, a</i> ; Odonata, <i>n, a</i> ; Orthoptera; Plecoptera, <i>n, a</i> ; Psocoptera.
<i>2sps-ils</i>	Coleoptera, <i>l</i> ; Megaloptera, <i>l</i> ; Neuroptera, <i>l</i> .
<i>2sps-cx₁</i>	Thysanura; Blattariae; Coleoptera, <i>l</i> ; Grylloblattodea; Isoptera; Mantodea; Megaloptera, <i>l</i> ; Neuroptera, <i>l</i> ; Odonata, <i>n, a</i> ; Orthoptera; Plecoptera, <i>n, a</i> ; Psocoptera.
<i>2sps-cx₂</i>	Thysanura; Blattariae; Coleoptera, <i>l</i> ; Dermaptera; Grylloblattodea; Isoptera; Megaloptera, <i>l</i> ; Neuroptera, <i>l</i> ; Odonata, <i>n, a</i> ; Orthoptera; Plecoptera, <i>n, a</i> ; Psocoptera.
<i>2sps-3sps</i>	Thysanura; Blattariae; Mantodea.
<i>3sps-3ils</i>	Thysanura; Coleoptera, <i>l</i> ; Mallophaga; Mecoptera; Megaloptera, <i>l</i> ; Phasmatodea.
<i>3sps-fu₁</i>	Thysanura; Blattariae; Ephemeroptera; Isoptera; Mallophaga; Mantodea; Mecoptera; Megaloptera, <i>l, a</i> ; Neuroptera, <i>a</i> ; Orthoptera; Phasmatodea; Psocoptera.
<i>3sps-s₁</i>	Thysanura; Megaloptera, <i>l</i> .
<i>3sps-ils</i>	Thysanura; Blattariae; Isoptera; Mantodea; Megaloptera, <i>l, a</i> ; Orthoptera; Psocoptera.
<i>3sps-2ils</i>	Coleoptera <i>l</i> .
<i>3sps-cx₁</i>	Thysanura; Coleoptera, <i>l</i> ; Grylloblattodea; Isoptera; Mantodea.
<i>3sps-Isps</i>	Thysanura ?; Blattariae ?

Glossary of abbreviations

<i>ax</i>	axillary sclerite
<i>cv</i>	cervical sclerite
<i>cx</i>	coxa
<i>cps</i>	episternum
<i>fu</i>	furca, furcal arm, segmental sternal apophysis
<i>ils</i>	intersegmental laterosternite
<i>lig</i>	intersegmental transverse ligament
<i>pl</i>	pleuron
<i>s</i>	segmental sternum
<i>sps</i>	spinasternite or spina
<i>X</i>	cruciate, used of a muscle whose origin and insertion are on opposite sides of the midline

DISCUSSION OF MUSCLE TYPES

The spinasternal muscles considered here include four main types: (a) the transverse muscles; (b) oblique muscles attached on the furcal arms (*fu*) or on the intersegmental laterosternites (*ils*); (c) spinacoxal muscles; and (d) spinaspinal muscles. In some species, spinasternal muscles with attachments other than those just indicated are found, but these can usually be interpreted as derived from one of the types already listed. Exceptions are the spinaternal muscles of some Apterygota (Maki, 1938; Barlet, 1953, 1954) and the spinal depres-

sors of the trochanter in Diplura (Maki, 1938), which seem not to occur in any pterygote insect. They are omitted from this discussion mainly because of the relative scarcity of information about their distribution and exact structural relationships.

a. *Transverse spinal muscles:*

1. <i>1sps-1ils</i>	<i>2sps-2ils</i>	<i>3sps-3ils</i>
2. <i>1sps-cps₂</i>	<i>2sps-cps₃</i>	...

1. Two kinds of transverse muscles are recognized here. The first is inserted laterally on the *ils* in each intersegment, and is either attached medially on the corresponding spina, or passes directly across the body to the *ils* of the opposite side. Examples of the latter condition are found in the first thoracic intersegment in adult Neuroptera (Czihak, 1956), in the trichopteran *Stenopsyche* (Maki, 1938, muscle No. 32), and perhaps by the same author as muscle No. 20 in *Ctenacroscelis* (Tipulidae). It is also possible that the muscle recorded as number 56 by Maki (1938) in the mecopteran *Neopanorpa* is of this type. A similar arrangement exists in some Odonata, but in others the muscle has been replaced by a sclerotized bridge that runs across the body, as is also the case in the second thoracic intersegment of these insects (Maloeuf, 1935; Maki, 1938; Clark, 1940). Even when the first type of transverse muscle is not replaced by sclerotization, it is frequently ligamentous.

The first type of transverse muscle has also been noted, as *1cv-1cv*, in the cervical intersegment of *Myrmeleon* (Czihak, 1956; *M. intercervicalis*), and is probably represented as part of the "tentorium col-laire" of Iepismatids (Barlet, 1951); in neither case is there a median attachment. The medial connection to the integument is present in the third thoracic endosternum of Thysanura (Barlet, 1951), but is of course ordinarily absent here in Pterygota, where postmetathoracic transverse muscles or ligaments occur in some coleopterous larvae (Speyer, 1922; Chadwick, unpublished), Mallophaga (Mayer, 1954), Mecoptera and Phasmatodea (Maki, 1936, 1938). In Collembola the third spina is preserved, so that the muscle actually appears as *3sps-3ils*, (Maki, 1938, No. 87 in *Neanura*, No. 83 in *Folsomia*). In larval *Corydalus*, the ligament that corresponds to *3sps-3ils* extends inward from *3ils* and supports some of the longitudinal ventral muscles, but fails to reach the median junction identified as "*3sps*" by its reception of other muscles of the third spina. As already noted, transverse muscles of the abdominal intersegments have been found in many insects; see Ford (1923); Maki (1938); Chadwick (1957).

2. The second type of transverse muscle listed occurs only in the

first and second thoracic intersegments. It is seldom ligamentous, and its lateral insertion is on the anterior margin of the immediately succeeding episternum. Unlike the first type, it rarely lacks the median attachment, though in *Cryptocercus* (Blattariae) the more dorsal fibers of $1sps-eps_2$ are found as eps_2-eps_2 (Chadwick, 1957), while in *Cyclochila* (Homoptera) the muscle that apparently corresponds to $1sps-eps_2$ has no midventral insertion (Larsén, 1945c).

While this second type of transverse muscle may be ultimately a derivative of the first, which represents the usual transverse intersegmental muscles of arthropods, there is evidence that both types have existed independently for a very long time in the hexapod line. Thus, there are in *Lepisma* two such ligaments, n and n' of Barlet (1951), in the first thoracic intersegment. *Cryptocercus* (Blattariae) has two transverse muscles, the anterior partly ligamentous, in both the first and second intersegments, while a similar arrangement is found in the first intersegment of some Isoptera (Chadwick, 1957; idem, unpublished), and in both intersegments of certain sialids (Czihak, 1953; Chadwick, unpublished). Elsewhere, only one or the other of the two types is seen; and in some mantids the data suggest that the same muscle which in immature forms is attached on *ils* may appear with the episternal attachment in the adult.

Several authors have listed as transverse muscles the bands fu_1-fu_1 , fu_2-fu_2 , fu_3-fu_3 , whose proper affinity seems rather to be with the spinafurcal muscles, as explained in the next section. Yet, a difficulty in regard to this interpretation arises in the mallophagan genera *Trimenopon* and *Myrsidea*, where Mayer (1954) has described two transverse muscles of the third thoracic intersegment. One of these, *III trm 1*, is stretched between opposite sternal arms in the usual manner and probably represents a former spinafurcal muscle, $3sps-fu_3$. The other, *III trm 2*, arises on fu_3 and is inserted medially on the membrane between metathorax and abdomen, i.e., at the presumed locus of a third spina. Now, if the first band, fu_3-fu_3 (*III trm 1*), of these Mallophaga is to be taken as comparable with the similarly located muscles and ligaments of other insects, then *III trm 2* must represent a different muscle, and this could be only $3sps-zils$. This assumption, which seems the simplest that will account for the facts, is however not wholly satisfactory, for it forces us to suppose too that fu_3 and $zils$ were at one time contiguous, in order to facilitate the transfer of the attachment of *III trm 2* from $zils$ to its present location on fu_3 . Such a contention is at present without the support of any other evidence, and indeed seems rather unlikely. Moreover, while

we know of a few instances where muscle attachments have been shifted between parts that could never have been contiguous, this seems to have occurred very rarely. It is probable, therefore, that only a developmental investigation offers hope of solving the problem at issue here. However, it is worth noting that a phasmid, *Megacrania*, actually has two transverse muscles of the third intersegment (Maki, 1935): No. 140, which is my fu_3-fu_3 , and hence interpreted here as the equal of $3sps-fu_3$; and No. 234, which is $zils-zils$, interpreted by me as derived from $3sps-zils$.

b. *Oblique spinal muscles of the furca and intersegmental latero-sternites:*

3. $1sps-fu_1$	$2sps-fu_2$	$3sps-fu_3$
4. $1sps-zils$	$2sps-zils$	$3sps-lils$
5. $1sps-fu_2$	$2sps-fu_2$	$3sps-s_1$
6. ...	$2sps-lils$...
7. ...	$2sps-lils$...
8. ...	$2sps-fu_1$	$3sps-fu_2$
9. ...	$2sps-lils$	$3sps-zils$
10. ...	$2sps-pl_1$	$3sps-pl_2$

3. A muscle from each spina to the preceding furca was characteristic of the early hexapods, to judge by the wide representation of such muscles among existing orders (table 1). However, a tendency toward modification and loss of these muscles is also apparent. Though all three muscles are lacking only in higher Diptera and adult Coleoptera, one or another of them has disappeared without trace in all but seven orders, and their occurrence elsewhere may vary with the species.

In many instances, loss of the spinasternal attachment has evidently converted the formerly paired muscles, $1sps-fu_1$, etc., into a single band, fu_1-fu_1 , etc. (see, for example, Badonnel, 1934, on *Stenopsocus*). Moreover, since the furcal arms of the same segment are often nearly immovable relative to each other, one finds that the muscular bands, fu_1-fu_1 , etc., are frequently replaced by ligamentous straps, or even (in Odonata, some Hymenoptera) by sclerotized braces. For the details in most orders, reference will have to be made to the list of original sources above; but we would reemphasize here our conviction that the so-called interfurcal muscles fu_1-fu_1 , etc., are morphologically distinct from the true transverse intersegmental muscles, such as $1sps-lils$ or $1sps-eps_2$, and that the interfurcal muscles are most probably derived from the type $1sps-fu_1$, etc.

As explained in section 2 above, we have chosen tentatively to interpret the muscle *III trm 2* of some Mallophaga (Mayer, 1954), which has the form $3sps-fu_3$ as really representing $3sps-zils$; if this view is

correct, *III trm 1* of these species, which is fu_3-fu_3 , is comparable with the interfurcal muscle in other insects and hence with the presumed ancestral muscle $3sps-fu_3$, as well as with serial homologues in the more anterior segments. An alternative hypothesis would be to take *III trm 2* at face value, as being $3sps-fu_3$. The muscle *III trm 1* would then have to be interpreted as equivalent to $3sps-3ils$, which would pose the same requirement for a transient fusion of *3ils* and fu_3 to which we have objected above, and would also leave the status of *I trm* (fu_1-fu_1) and *II trm 1* (fu_2-fu_2) in doubt. We have rejected the alternative for this reason.

4. Only rarely is the spina connected by a muscle to the *ils* of the following intersegment, except for a band from the third spina or its equivalent to the *ils* between the first and second abdominal intersegments, i.e., to *Iils*. Such a muscle, $3sps-Iils$, is known to be present in the Thysanura and 7 pterygote orders; but since the vestiges of the third spina are not always recognized as such, and because of some confusion as to the identity of the anterior abdominal sterna, what may be the same muscle may have been described in different terms in some other groups and hence overlooked in this discussion.

Lepisma has equivalent muscles in all three thoracic segments (Barlet, 1953, Nos. 34, 42, 51); larval dytiscids, in two (Speyer, 1922, *II4d*, *III4d*; Chadwick, unpublished). In Dermaptera, the muscle $1sps-2ils$ (Maki, 1938; No. 28 in *Anisolabis* and *Labia*; Chadwick, unpublished, in *Forficula*) is obviously the functional substitute for $1sps-fu_2$, which is lacking here just as $1sps-2ils$ is in most pterygote insects. Larval *Corydalus* (Megaloptera) possesses a muscle, distinct from its $2sps-fu_3$, that runs from *2sps* to the intersegmental ligament, lig_3 , which is in this form the equivalent of $3sps-3ils$, as noted in section 1 above. This muscle, $2sps-lig_3$, evidently stands in this situation for $2sps-3ils$, and appears to have furnished part of $2sps-Iils$ in the adult (see section 6). Kelsey's (1957) description of *Corydalus* does not recognize the existence of larval lig_3 and $2sps-lig_3$, nor of adult $2sps-Iils$.

It is probable that the muscles numbered 29 in *Lepidocampa* and 24 in *Neanura* by Maki (1938) are serial homologues of the type under discussion, and represent a $osps-Iils$ that is not found in other insects.

Other examples of the occurrence of muscles of this nature are less certain. According to Maloeuf (1935), nymphal and adult dragonflies have a muscle (his No. 68) which may represent our $2sps-3ils$, and this may correspond to the muscles numbered 43 by Maki (1938)

in *Psolodesmus* and *Crocothemis*. Whether this also corresponds to Clark's (1940) *III vlm 2* is not sure. Walker's (1938) description of *Grylloblatta* gives the attachments of his No. *111b* as *2sps-3ils* (in our notation), but it is probable that the second abdominal sternum has been indicated as the first, in which case *111b* is really *2sps-1ils*. The muscles *I vlm 3* and *II vlm 4* of Korn (1943) in larval *Myrmeleon* (Neuroptera) may include portions equivalent to *1sps-2ils* and *2sps-3ils*, respectively, as well as parts identifiable as *1sps-fu₂* and *2sps-fu₃*. The exact relationships are doubtful. In the adult of this species all these muscles have disappeared (Korn, 1943; Czihak, 1956).

5. In contrast to the narrow distribution of the oblique spinal muscles of the *ils*, the absence of a muscle from the spina to the following furca is quite unusual. Thus, for example, *1sps-fu₂* is unknown only in the Odonata, Ephemeroptera, Phasmatodea, Mallophaga, Dermaptera, Hymenoptera, Diptera, and possibly in Hemiptera. With the exception of the Dermaptera which, as we have seen, appear to have retained *1sps-2ils* in place of the more usual *1sps-fu₂*, these groups have all undergone extensive modification of the anterior ventral region of the thorax, and the absence of *1sps-fu₂* is probably related to the skeletal changes that have occurred. In some of these insects, the first spina has been lost, and elsewhere it has often seemingly disappeared, through fusion with other exoskeletal or endoskeletal parts.

This same list of orders, again excepting the Dermaptera, lacks the corresponding metathoracic muscle, *2sps-fu₃*. In addition, this muscle has vanished, as far as is known, from the Thysanoptera, Homoptera, and Hemiptera; and from the series Mecoptera, Trichoptera, and Lepidoptera. In Neuroptera, it is absent from adults, though present in the larva of *Myrmeleon* (Korn, 1943). Possibly study of larval Mecoptera would also disclose a larger number of spinasternal muscles than is now known to occur in this order. Additional work on nematoceros Diptera is also needed, for while they, like other flies, seem to lack all true spinae, it is impossible to decide from Maki's (1938) description of *Ctenacroscelis* just which spinasternal muscles may have been preserved in what he refers to (pp. 244, 248) as "a common net of ventral transverse muscles."

A homologue, *3sps-s1*, from the third spina to the first abdominal sternum, which of course lacks a sternal arm, is known only from *Thysanura* (Barlet, 1953, No. 52) and from larval *Corydalus* (Chadwick, unpublished). In the megalopteran, the muscle runs from the common junction ("*3sps*") of spinasternal muscles of the third inter-

segment to an apodeme at the base of the first abdominal appendage. If the muscle in question is truly homologous with *1sps-fu₂*, *2sps-fu₃*, as seems likely, the apodeme of attachment is to that extent homologous with the sternal arms of the thoracic segments.

6 and 7. The muscles listed under these numbers are of such infrequent occurrence that one is persuaded to look elsewhere for their derivation, as will be explained presently; yet *2sps-lils* is characteristic of cockroaches, where it was described as *2sps-s_{1A}* by Chadwick (1957, No. 21). He accepted its equivalence to No. 111*b* of Walker (1938) in *Grylloblatta*, for reasons that have been given in section 4 above. Elsewhere, the muscle has been noted only in adult *Corydalus*; it is not present as such in the larva of this species (Chadwick, unpublished).

The same author (1957) has outlined how, in certain cockroaches, *2sps-lils* may give rise to *2sps-IIils* by incorporating an additional segment of the abdominal longitudinal ventral musculature. Though the resulting muscle has not been found in any other insect, so that it seems peculiar to cockroaches, the here evident mode of its formation suggests a possible origin for other long muscles, such as its parent, *2sps-lils*. The latter could easily have arisen through coalescence of *2sps-3ils* with *3ils-lils*, both of which muscles are of types serially repeated through several segments in primitive insects (for *2sps-3ils*, see section 4 above). The facts observed in *Corydalus* make it certain that this process is what takes place. The immature form of this insect has muscles *2sps-lig₃*, the equivalent of the more usual *2sps-3ils*, and *lig₃-lils* (for *3ils-lils*), but lacks *2sps-lils*, which comes into existence, as mentioned above, only in the adult. Now, the larval muscles suspended on *lig₃*, which is in this insect the partial equivalent of *3sps-3ils*, have already dissolved their formerly direct attachments to the integument and are therefore, so to speak, floating in the body cavity. During metamorphosis, the ligament finally disappears, and what was two muscles joined end to end becomes a single element.

We believe then that *2sps-lils* has been formed from *2sps-3ils* by simple addition of one segment of body musculature, just as *2sps-IIils* in cockroaches was derived from *2sps-lils*, as shown previously. We have outlined the process in some detail, not only because of its intrinsic interest, but also because it seems likely that it is a model for the derivation of certain other spinasternal muscles, some of which are to be discussed in section 10 below.

8. A muscle from the second spina to the first furca has been described from 12 orders (table 1) and may therefore be regarded as a

reasonably certain component of the ancestral pattern, even though it does not invariably occur in all species of the groups in which it is found. In Thysanura, we identify Barlet's (1953) No. 37 with this muscle, since No. 37 is attached on what seem to be appropriate portions of the first and second thoracic endosterna and passes ventral to the transverse ligaments n and n' . Further comment on the muscle $2sps-fu_1$ may be restricted to the statements that, although it is not found in larval dytiscids (Speyer, 1922; Chadwick, unpublished), it does occur, together with $2sps-ils$, in larval *Corydalus* (Megaloptera) (Kelsey, 1957; Chadwick, unpublished); and that in Neuroptera it is known only from larval *Myrmeleon* (Korn, 1943, No. *Iism*₃).

The serial homologue, $3sps-fu_2$, has been found among Pterygota only in the larva of *Cybister* (Chadwick, unpublished). Apparently this muscle is absent in the closely related larva of *Dytiscus* (Speyer, 1922). In Thysanura, Barlet (1953) has indicated that muscle No. 45 is the serial homologue of No. 37; hence we interpret No. 45 as equivalent to $3sps-fu_2$. A still more posterior homologue (No. 55 of Barlet, 1953), which would be $Isps-fu_3$ in our notation, has not been identified in other insects.

9. The muscles from the second and third spinae to the respective preceding *ils* are seldom found. No apparent equivalent is seen in Thysanura, but Maki (1938) has described in a dipluran, *Lepidocampa*, two muscles (Nos. 47 and 67) that probably belong here. Muscles similar to both of these occur in larval *Cybister* (Chadwick, unpublished); in larval *Dytiscus* only the anterior is found (Speyer, 1922, No. *II4e*), as in larval *Myrmeleon* (Korn, 1943, No. *Iism*₃) and in larval *Corydalus* (Kelsey, 1957; Chadwick, unpublished).

From the little that is known of these muscles we can infer only that they probably represent a primitive part of the hexapod pattern that began to disappear at a relatively early date, and that they are distinct morphologically from $Isps-fu_2$ and $2sps-fu_3$, as shown by their simultaneous occurrence with these muscles in certain primitive forms, as well as by the fact that the furcal muscles must pass beneath the transverse muscles, and hence beyond the *ils*, in order to reach their anterior site of attachment.

10. The pleuro-endosternal muscles of Thysanura (Barlet, 1953, Nos. 59, 60, 61,) are not included in table 1 but are considered here because their posterior attachment is on a region of the endosternum that evidently corresponds with the spina of Pterygota. They are known only from *Lepisma*. The spinal attachment of No. 61, $Isps-pl_3$, is abdominal. As Barlet (1953, p. 229) has suggested, these muscles

were probably formed "by the secondary union, end to end, of fibers which initially did not extend beyond the length of one segment." For lack of further evidence, Barlet refrains from any guess as to the probable components. It is noteworthy that these long muscles course ventrad of both the pleuro-endosternal and transverse intersegmental ligaments, a fact that does not facilitate interpretation of how they came into being. Nevertheless, we may accept Barlet's surmise as to their origin as probably correct in principle, the more so since we have seen, in sections 6 and 7 above, other similar examples of the formation of muscles more than one segment in length. One is tempted to seek the missing *2sps-ils*, *3sps-2ils*, etc. (section 9) in the long pleuro-endosternal muscles of *Lepisma*, but this is pure conjecture that might furthermore meet some topographical difficulties. An embryological study of *Lepisma* would furnish an unexploited opportunity of obtaining evidence on the question.

c. *Spinacoxal muscles*:

11. <i>1sps-cx₁</i>	<i>2sps-cx₂</i>	<i>3sps-cx₃</i>
12. <i>1sps-cx₂</i>	<i>2sps-cx₃</i>	...

11. In some 13 to 15 orders, each spina, with exception of the often missing third, serves as a point of origin for a spinal remotor of the immediately preceding coxa. Serial homologues of these muscles have been found even for the third coxa in 8 or 9 orders, and may be yet more widely represented, as Maki (1938) has suggested, in the definitive posterior furcal rotators of some species. Badonnel's (1934) study of the innervation of the corresponding furcocoxal muscles in *Stenopsocus* tends to support this view.

It is worth remarking that in Thysanura two separate spinal remotors are found for each coxa (Barlet, 1954, Nos. 99, 100; 110, 111; 116, 117). Maki (1938) noted a double spinal remotor of the first coxa in *Locusta* (Nos. 25, 26). A somewhat similar situation occurs in all three segments of larval dytiscids (Speyer, 1922; Chadwick, unpublished), where one band originates on the spina or its equivalent while the second originates on the corresponding *ils* and thus crosses the contralateral homologue on its way to the insertion in the opposite coxa. Larval *Corydalus* (Megaloptera) also has a cruciate coxal remotor, as well as the usual spinal remotor, in the second and third segments; but here the cruciate muscles originate on the respective furcal arms (Chadwick, unpublished). The cruciate muscles are no longer found in the adult of this species or in a North American species of *Sialis*, but Czihak (1953) has noted three remotors of the first coxa in *Sialis flavilatera* L. Two of them (*Mm. spino-coxales*)

originate on *isps*; the other (*M. postpleurocoxalis transversus*) is a cruciate muscle that originates on *ils*. This arrangement is essentially what is seen in certain cockroaches, while others appear to have double spinal remotors, *isps-cx₁*, instead (Chadwick, 1957).

From all these indications, the probability is that the intersegmental coxal remotors of pterygote insects were at one time more diverse than they ordinarily appear to be in those species in which they are preserved. It is not possible, however, to decide on the basis of present data precisely how the spinal muscles and the cruciate muscles may be interrelated (see section 12, below).

Another most interesting development is the apparent substitution, in Neuroptera, of a mesosternal remotor of the first coxa for the typical spinal remotor (Korn, 1943; Czihak, 1956; Chadwick, unpublished). According to all these authors, the definitive remotor originates near the midline at the junction of the prosternum and mesosternum. Chadwick found that this muscle in adults of an unidentified American species passes ventrolateral to the nerve cord, a significant detail that has now been confirmed for the European forms, both larval and adult, by Czihak (in lit.). Thus, despite the attachment on what has been identified as the spina in larval *Myrmeleon* (Korn, 1943) and in adult *Ascalaphus* (Czihak, 1956), the remotor in Neuroptera lacks one of the customary characteristics of all true spinasternal muscles. Yet it seems likely that the muscle in Neuroptera is the homologue of the spinasternal remotor found in other insects, if only because there is no other evident source from which the Neuroptera could have derived it; and still one must grant that the transfer, in phylogeny or ontogeny, of a muscle attachment across one of the principal nervous connectives is a most unusual event. If this is what has occurred, we must also consider that what has happened once may happen again, so that we have no guarantee that muscles that are truly spinasternal in one form cannot be homologues of muscles with only paraneural attachments in another. The fact is, of course, that it is the rarity of such shifts that should be emphasized in the present state of our knowledge.

12. Spinal promotors of the second and third coxa occur in about as many orders as the corresponding remotors, though the pattern of distribution is somewhat different (table 1). In Thysanura, the promotors also are double (Barlet, 1954, Nos. 106, 107; 112, 113); but they are not so noted in other species, except in the metathorax of larval *Dytiscus* (Speyer, 1922, No. III 17).

Apparent equivalents of the spinal promotors of the mesocoxa were

reported by Mayer (1954) in four genera of Mallophaga, as muscle No. *II trm 2*, which she describes as cx_2-cx_2 ; i.e., the former spinasternal attachment has been lost. The promotors are not known to occur in this form in any other group of insects.

One naturally wonders whether there exist prothoracic homologues of the spinacoxal promotors of the second and third legs. Maki (1938) may have found them in Collembola (*Neanura*, No. 38) and Diplura (*Lepidocampa*, No. 36). Other insects apparently have no structure that stands in place of a cervical spina, so that searching elsewhere for strictly homologous muscles would seem fruitless. Nevertheless, Badonnel (1934) considered the cruciate cervical promotor, $1cv-cx_1X$ in my notation, of *Stenopsocus* (No. X_1) serially homologous with the spinal promotors that he found in the pterothorax. His conclusion was based partly on the similar innervation. Barlet (1954) has regarded the cruciate coxotentorial muscles (Nos. 99, 100) of *Lepisma* as serial homologues of the spinacoxal promotors of the mesothorax and metathorax (Nos. 106, 107; 112, 113; respectively).

Now, cruciate cervicocoxal muscles, undoubtedly homologous with those of *Stenopsocus* and *Lepisma*, have been described from nine other orders, all among the Pterygota. These muscles may surely be looked upon as functional replacements for the missing prothoracic spinal promotors, but one doubts that they can be wholly homologous with them in the morphological sense. The resolution of this question should hang together, it seems, with one's interpretation of the possible homology between spinal and cruciate remotors (see section II above); and here the evidence, such as it is, does not favor the proposed homology. A major stumbling block is the fact that both types of remotors are sometimes found in the identical segment. Although this is not yet the case for the promotors, one still cannot accept Badonnel's argument from the innervation, which is simply of the type characteristic of most intersegmental muscles and hence not decisive as to the point at issue. Nor can one agree with Barlet that the crossing point of the right and left coxotentorial muscles represents the missing cervical spina, for there are too many instances in other intersegments where cruciate muscles and authentic spinae exist together. Barlet's further suggestion, that the "long" coxotentorial muscles have been formed by coalescence of former spinacoxal muscles with some other spinal element, deserves consideration, but it again meets the old difficulty of explaining the coexistence of spinal and cruciate remotors in the same segment. Once again it seems that only

developmental studies offer hope of direct information as to the true relationships. Meanwhile, one had best recognize the existence of both types of muscle, while deferring an opinion as to their homology.

d. *Spinaspinal muscles:*

13. *1sps-2sps* *2sps-3sps* *3sps-1sps*

13. The spinaspinal muscles are limited in their known distribution to Thysanura (Barlet, 1953, Nos. 36, 44, and probably 54, in *Lepisma*) and to a few orthopteroid orders. Larsén's (1945c) citation of Speyer (1922) as an authority for their presence in larval *Dytiscus* is apparently an error.

The bands *1sps-2sps* are present in blattids (Chadwick, 1957, No. 12), in nearly all the true Orthoptera and Mantodea that have been studied, and in *Stenopsocus* (Badonnel, 1934, No. LVM2). Maki (1938) did not find them in *Psocus*. Chadwick (1957) failed to find these muscles in nymphal *Tenodera* (Mantodea), but did find vestiges of *2sps-3sps* there; this element is relatively well developed in cockroaches (No. 23). *Lepisma* is the only other insect in which *2sps-3sps* is known. Certain usually weak muscular strands that connect "3sps" of cockroaches with the ventral diaphragm may be serially homologous with the preceding spinaspinal muscles and with Barlet's No. 54 in *Lepisma*.

Given the absence of a *osps* in most insects, one is not surprised that the muscle *osps-1sps* is ordinarily missing. However, what may be this muscle has been recorded by Maki (1938) as No. 28 in *Lepidocampa* (Diplura), which seems to possess a cervical spina.

Originally, the spinaspinal muscles are paired bilaterally, but the two bands may coalesce during development to such an extent as to become indistinguishable. The present distribution of these muscles, as well as their location, suggests that their retention is a primitive characteristic, although they are notably absent in several otherwise unquestionably primitive forms.

CONCLUSIONS

Our principal conclusions have been anticipated to some extent in the manner of presentation of the data and in the discussion of individual muscle types. Thus, the mere fact that it is possible to construct such a summary as table 1 seems to establish the point that all the insects we have examined must be descendants of a common ancestral stock, whose spinasternal musculature included most of those elements that, as we have seen, are somewhat sporadically distributed among

the living representatives. A corollary of this interpretation is that individual muscles that we have listed are in most cases homologous throughout the orders and segments in which each occurs. Nowhere have we found evidence for the creation in phylogeny of wholly new spinasternal muscles; rather we have observed that the ruling tendency has been one of increasing restriction of the ancestral pattern as the more recently differentiated orders evolved. In those instances where there is a change in the complement of spinasternal muscles during ontogeny, one detects the same trend toward reduction of the spinasternal musculature that is so clearly manifest in phylogeny.

The spinasternal musculature also provides reasonably good indications that all three thoracic segments were at one time nearly identical in respect to it. Such relationships are not seen anywhere at present, for the proximity of the prothorax to the head and of the metathorax to the legless abdomen have dictated that the several thoracic segments should diverge in structure.

If we ignore the unusual spinaternal and spinatrochanteral muscles, whose distribution has not been sufficiently studied to allow their inclusion here, we may suppose that the typical body segment, for which we shall use the mesothorax as a model, originally had the following spinasternal muscles:

- | | | |
|-------------------------------|-------------------------------|-------------------------------|
| 1. <i>2sps-2ils</i> | 3. <i>2sps-3ils</i> | 6. <i>2sps-cx₃</i> |
| 2. <i>2sps-fu₁</i> | 4. <i>2sps-1ils</i> | 7. <i>2sps-3sps</i> |
| | 5. <i>2sps-cx₁</i> | |

From these seven basic types we can, with a fair degree of probability, derive all the known spinasternal muscles that have been considered above. The proposed derivations are summarized in the following paragraphs, which carry the same numbering as the corresponding muscles in the list just given.

1. The transverse muscle, typified by *2sps-2ils*, is thought early to have split off a second band with attachment on the anterior margin of the following subcoxa; i.e., the present *2sps-eps₃*. However, a derived muscle of this nature seems to have been confined to the first two thoracic intersegments. There is no indication that a corresponding postmetathoracic band ever existed; and if one developed in the cervical region, it was soon obliterated. In the pterothorax, modern insects may show either, neither, or occasionally both bands.

The muscle *2sps-2ils* and its serial homologues, *1sps-1ils* and *3sps-3ils*, have frequently been replaced by a ligament, apparently as a result of increasing sclerotization and consolidation of the thoracic segments. Loss of the spinasternal attachment, or disappearance of the

spina, may convert the still surviving muscle or ligament into the form *zils-zils*, or occasionally even *eps₃-eps₃*. In a few instances, sclerotization along the course of the ligament or former muscle has ended in complete fusion and the formation of an endoskeletal bridge.

2. The spina was regularly connected by a muscle with the immediately preceding furcal region. In many orders, a corresponding muscle, ligament, or fusion still persists, but in some this has disappeared without a trace. Some form of union has been preserved more often in the prothorax, a reflection no doubt of the greater degree of consolidation of the winged segments and of the reduction that has generally taken place in the anterior sternal region of the abdomen.

3. An oblique muscle connected the primitive spina with the following *ils*, but either a portion of this band soon became attached to the corresponding furcal arm or else an independent muscle, *zsps-fu₃*, already existed, for the furcal muscle is the more frequently represented in modern insects. The band *zsps-zils* is still found in a few, mainly larval forms; and both it and the furcal muscle are present together occasionally. By adding to itself the lateral longitudinal band, *zils-lils*, the oblique muscle has given rise, in three orders, to *zsps-lils*; and, by an extension of this process, to *zsps-llils* in one.

4. Another oblique muscle stretched between the spina and the preceding *ils*; as in the previous example, a part of this muscle, or an independent muscle, is now usually found attached to the corresponding furca, as *zsps-fu₁*. We may suppose also that addition of a pleuro-intersegmental element at the anterior end of the muscle *zsps-lils* yielded the long pleuro-endosternal muscle, *zsps-pl₁*, of *Lepisma* (Bartlet, 1954), though details of the origin of such muscles are still in doubt. A prothoracic homologue, *lsps-oils*, has not been described, while the also expected *lsps-fu₃* may sometimes be present though unrecognized among the usual furcabdominal muscles.

5 and 6. The spinacoxal muscles, both remotors and promotors, are still of frequent occurrence among insects. For the present, we have lumped with them the corresponding cruciate intersegmental coxal muscles, although these may originally have been independent entities. The usual origin of the cruciate muscles is on the *ils* of the opposite side. Those of the cervical intersegment originate on the *lcv*, on the "tentorium collaire," or partly on the postocciput, this last in some Mallophaga (Mayer, 1954). In a few acridids (Orthoptera), the insertion has been transferred from the procoxa to the profurcal arm. The cruciate remotors of the second and third coxae of larval *Corydalus* (Megaloptera) have shifted their origins to the respective furcal arms.

7. Spinaspinal muscles are only rarely preserved; but, as part of the original longitudinal body musculature, their presence must nevertheless be regarded as a primitive sign.

Although the spinasternal musculature thus gives evidence of a fundamental likeness among the thoracic segments, we must not overlook the fact that the three differ at present in many important respects. Their differentiation from one another began very early, under stress of the somewhat different forces to which each was subjected; and even the spinasternal musculature shows unmistakable traces of such effects. Our reconstruction of the basic spinasternal pattern affords but a glimpse into the state of affairs that prevailed before the functions and hence the structure of the present thoracic segments began to diverge; from this viewpoint our list may even be thought of as preinsectan in its nature. Certainly alterations specifically affecting the cervical region must have occurred in connection with the development of the characteristic architecture of the head, and these must therefore long antedate the emergence of the insects as a class. Changes in the anterior abdominal region must also have taken place very early, as an accompaniment of restriction of the locomotor function to the thorax.

It is the subsequent history of the spinasternal musculature that should help to illuminate the interrelationships of modern insects; and in Part II of this paper I have used the data here presented for such an analysis.

PART II. THE RELATIONSHIPS OF SOME ORDERS OF INSECTS, AS INDICATED IN THEIR SPINASTERNAL MUSCULATURE

Review of existing information on the spinasternal muscles of the Thysanura and 24 pterygote orders prompts the question, to what extent might this and similar knowledge be used to illuminate the interrelationships of the insects concerned?

The pertinent facts about these muscles have been given in detail in Part I of this paper, to which the reader is referred also for references to the original sources. As concluded in that study, all present-day orders are traceable ultimately to a single stock of insectan or preinsectan forms whose spinasternal musculature included not less than the 28 elements listed below in table 2. Of these elements, we find 27 represented in the Thysanura, 19 each in the Blattariae and Megaloptera, 16 each in the Orthoptera and Coleoptera (larval dytiscids); and so on, down to 1 in Hemiptera and 0 in brachycerous Diptera.

TABLE 2.—List of spinasternal muscles considered

<i>1sps-iils</i>	<i>2sps-2ils</i>	<i>3sps-3ils</i>
<i>1sps-eps₂</i>	<i>2sps-eps₂</i>	...
<i>1sps-fu₁</i>	<i>2sps-fu₁</i>	<i>3sps-fu₁</i>
<i>1sps-2ils</i>	<i>2sps-3ils</i>	<i>3sps-1ils</i>
<i>1sps-fu₂</i>	<i>2sps-fu₂</i>	<i>3sps-s₁</i>
...	<i>2sps-1ils</i>	<i>3sps-2ils</i>
...	<i>2sps-fu₁</i>	<i>3sps-fu₂</i>
<i>1sps-cx₁</i>	<i>2sps-cx₂</i>	<i>3sps-cx₃</i>
<i>1sps-cx₂</i>	<i>2sps-cx₃</i>	...
<i>1sps-2sps</i>	<i>2sps-3sps</i>	<i>3sps-1sps</i>

Also included are *1cv-cx₁X*, corresponding to *1sps-cx₂*, *2sps-cx₃*; and *1sps-3ils*, corresponding to *2sps-1ils*, *3sps-2ils*. See text.

NOTES TO TABLE 2.

1. The muscles *2sps-1ils*, *3sps-2ils*, and *1sps-3ils* are regarded as having provided parts of the definitive *2sps-pl₁*, *3sps-pl₂*, *1sps-pl₃*, respectively, in *Lepisma*; so that the form of muscles listed in the table is believed to be represented in thysanurans.

2. The muscle *2sps-3ils* is believed to furnish part of the definitive *2sps-1ils* in certain Pterygota. See text.

3. Ligamentous portions of the endosternum of *Lepisma*, as described by Barlet (1951), are taken to correspond to pterygote muscles or ligaments, as follows:

Barlet, 1951	This paper
<i>m-b-q</i>	<i>1sps-fu₁</i> , etc.
<i>n</i>	<i>1sps-iils</i> , etc.
<i>n'</i>	<i>1sps-eps₂</i>

Glossary of abbreviations

<i>cv</i>	cervical sclerite
<i>cx</i>	coxa
<i>eps</i>	episternum
<i>fu</i>	furca, furcal arm, segmental sternal apophysis
<i>ils</i>	intersegmental laterosternite
<i>m-b-q, n, n'</i> ..	parts of endosternum of <i>Lepisma</i> (Barlet, 1951)
<i>pl</i>	pleuron
<i>s</i>	segmental sternum
<i>sps</i>	spinasternite or spina
<i>X</i>	cruciate, used of a muscle whose origin and insertion are on opposite sides of the midline

The abbreviations are used throughout the text to form designations of the various muscles discussed, by placing a hyphen between abbreviations for the structures between which the muscle is stretched. Subscripts, arabic for the thorax and roman for the abdomen, indicate the segmental affinity. Intersegmental structures are preceded by the appropriate numeral, beginning with 0 for the cervical intersegment and 1 for the first abdominal intersegment. The customary designations, *1cv*, *2cv* . . . etc., for the cervical sclerites are retained.

Thus we see that there has been a continuing reduction in the number of these muscles with the differentiation of the more recent orders. Apparent also is the likelihood that the individual muscular elements are homologous throughout the numerous species in which each occurs, for the presence of each muscle in several only distantly related forms makes any other explanation very improbable. Nowhere has evidence been found for the late acquisition or development of new spinasteral muscles, except through modification of those already existing. One sees, instead, that spinasteral muscles have sometimes disappeared in phylogeny, or have been replaced with skeletal parts, whereas the reverse seems not to have occurred. Similarly, an attachment once lost or dissolved is not regained in the descendants of that stock.

These observations and inferences from them encourage one to proceed with an analysis of relationships, on the assumption that any group of insects that today possesses a certain muscle cannot have inherited it from one lacking the muscle in question. The converse of this proposition is of course false: common possession of a given muscle or pattern cannot guarantee any close genetic tie between the two groups concerned. The approach from this angle is therefore essentially negative, but it is nevertheless useful in showing that some relationships proposed are clearly impossible while others are still open for consideration. While it is improbable that any existing order of insects is the direct offshoot of any other group now living, bearing this in mind evidently does not exclude the possibility that, as far as mere numbers are involved, a present pattern of the spinasteral musculature could have been derived from one like that now manifest in some other order.

Examination of our data from the viewpoint set forth above shows the following:

1. At least 9 orders are surely of independent origin, in the sense that none of them is traceable directly to any other order now extant. These are the Thysanura, Blattariae, Megaloptera, Orthoptera, Coleoptera, Psocoptera, Mantodea, Grylloblattodea, and Neuroptera.

2. The spinasteral pattern of Dermaptera, Odonta, and Mallophaga could have been derived directly from a pattern like that now represented in the Thysanura, but not from any other existing group. However, certain elements interpreted by me as spinasteral occur in modern Thysanura as ligamentous portions of the endosternum (see table 2, notes). Since in pterygote insects the presumed homologues of these parts are in many instances contractile muscles, these must be assumed to have been inherited from a prethysanuran form in which

the elements were still definitely muscular. Thus, the thysanuran pattern may be ancestral to that found in certain pterygote groups, but the present Thysanura cannot stand in the direct line of pterygote descent.

3. The Megaloptera are the only existing order with a pattern that might be ancestral to that of the Isoptera. Inasmuch as there are good grounds for postulating an entirely different origin for the termites, the similarities observed here must be put down to the fortuitous retention by both groups of a number of the same primitive characteristics.

4. The remaining orders have patterns derivable by simple reduction from both the thysanuran type and that of one or more other orders, as follows: Plecoptera, from Blattariae; Mecoptera, from Odonata; Phasmatodea, from Mecoptera and Mallophaga; Hymenoptera and Embiodea, from Orthoptera and Psocoptera; Trichoptera, from Blattariae, Megaloptera, Coleoptera, Psocoptera, Isoptera, and Plecoptera; Lepidoptera, from the same orders as Trichoptera, plus Orthoptera and Trichoptera; Ephemeroptera, from Orthoptera, Psocoptera, Neuroptera, Mecoptera, and Phasmatodea; Thysanoptera, from the same orders as Lepidoptera, plus Neuroptera and Lepidoptera; Homoptera, from Thysanura, Blattariae, Megaloptera and Isoptera. To these should be added Coleoptera, Psocoptera, Plecoptera, and Trichoptera, if the muscle described by Larsén (1945c) is *isps-ils*; but only Orthoptera and Grylloblattodea if this muscle is *isps-eps*. Hemiptera could be derived from all the foregoing orders except Mantodea, Neuroptera, Ephemeroptera, and Thysanoptera.

This tabulation reveals incidentally that, in general, the number of possible paths of derivation increases as the number of spinasternal muscles decreases, without necessarily indicating genetic relationships. The need for other criteria therefore grows as the number of spinasternal muscles diminishes.

5. The brachycerous Diptera, for which several species have been studied, apparently lack all spinasternal muscles.

The conclusions drawn above can be set down with confidence from simple comparison of the spinasternal muscles of the different orders. In proceeding beyond this point in the attempt to understand insect relationships, it is necessary to resort to logical though hypothetical reconstruction of presumed ancestral spinasternal patterns. A few examples will clarify what can be learned in this way.

Of the 14 muscles that constitute the spinasternal pattern of Psocoptera, only one, *isps-ils*, is missing from Orthoptera. However, this same muscle occurs in 10 other pterygote orders and in the Thy-

sanura, so that it is reasonable to suppose that it must also have been present relatively recently in the ancestry of the Orthoptera. But a form that possessed this muscle in addition to those already found in the present Orthoptera could serve as a potential direct ancestor for both the Orthoptera and Psocoptera, for the various other orders now theoretically derivable from them, namely, the Hymenoptera, Embiodea, Trichoptera, Lepidoptera, Ephemeroptera, Thysanoptera, Homoptera, Hemiptera, and Diptera; and for the Plecoptera.

Similar small changes would allow the inclusion of yet other groups. The hypothetical composite that we have formed, with its 17 muscles, contains only one element, $2sps-fu_2$, that is not found in the present blattid pattern of 19 muscles. But, although this element is missing in present-day cockroaches, the muscle $2sps-fu_2$ is known from 11 other pterygote orders and the Thysanura, and it is matched in the blattids by the serial homologues $1sps-fu_1$ and $3sps-fu_3$. Cockroach ancestry must have had $2sps-fu_2$. Almost certainly, too, the ancestral blattids must have possessed a distinct $3sps-cx_3$, which occurs in several other primitive groups and is apparently still represented in existing cockroaches as a portion of the thus transformed fu_3-cx_3 (Badonnel, 1934; Maki, 1938; Chadwick, 1957). Now, the addition of only these two muscles, $2sps-fu_2$ and $3sps-cx_3$, to the present blattid complement creates a composite of 21 muscles, from which could be derived the existing patterns of the Isoptera, Mantodea, and Grylloblattodea, in addition to those of all the groups already mentioned as possible descendants of the Blattariae and of the combined Orthoptera and Psocoptera.

The steps thus outlined dispose of all those more or less primitive orders, possessing upward of nine spinasternal muscles, that are most like what we shall designate for brevity as the orthopteroid stock; and the small number and logical nature of the changes proposed show that these orders probably form a natural and relatively closely knit group.

Turning to the remaining orders, we see that in general those groups with more than four spinasternal muscles share some tendency toward retention of a greater proportion of muscles with attachments on the *ils*, and of muscles of the third spina, while they lack spinaspinal muscles. Apart from these similarities, which are by no means expressed universally among them, these orders are rather diverse in spinasternal structure; and there is thus good reason for thinking that many of them are only distantly related to one another and to the series of orders already considered.

An exception to these generalizations may perhaps be exemplified in the Dermaptera, which are often looked on as orthopteroid insects. In fact, the Dermaptera could be derived directly from our orthopteroid-psocopteroid composite, with its 17 spinasternal muscles, did they not possess a *Isps-2ils* that has not been found in any of the orthopteroid orders that we have considered. Among the latter, *Isps-fu₂* usually stands in place of the *Isps-2ils* of the Dermaptera, and it may be that the two elements are really homologues in this instance. But, whether one is inclined to equate the *Isps-2ils* of Dermaptera with the *Isps-fu₂* of other insects, or to accept its apparent equivalence to the *Isps-2ils* of Thysanura, Megaloptera, Coleoptera, and Neuroptera, in some of which both muscles occur together, it becomes obvious that the Dermaptera have struck out on a morphological path that has been followed by no other orthopteroid group. At least to this extent then, the Dermaptera have set themselves somewhat aside from the main line of orthopteroid descent.

Among the orders yet to be considered are those that are usually referred to as neuropteroid, and of them we have for the Megaloptera, Coleoptera, Neuroptera (s.s.), and Mecoptera sufficient data to warrant discussion. There has been some question as to whether the Coleoptera should be included with these other groups, but the similarities in the spinasternal musculature of larval dytiscids and Megaloptera are decisive on this point. Adult Coleoptera, however, have progressed to such a degree of thoracic specialization that at most two spinasternal muscles are left, and the majority of beetles are thus without diagnostic value in the present context.

As already indicated, the neuropteroid orders, as I shall continue to call them, make up a somewhat looser aggregate than we have seen in the orthopteroid groups. The Megaloptera, Coleoptera, and Neuroptera, which are the more primitive among them, agree in lacking the cruciate cervicocoxal muscle, *Icv-cx₁X*, which is characteristically present in equally primitive orthopteroid orders; but this same muscle comes to light again in the Mecoptera, which have but seven spinasternal muscles in all. Thus we must choose either to exclude the Mecoptera from the neuropteroid series, or else to postulate that *Icv-cx₁X* was present at the base of the stem from which the Mecoptera were derived after the branches leading to the Megaloptera, etc., had been given off. The second of these alternatives seems to accord better with other data and is therefore the one adopted here, although it implies that the stock that produced the Mecoptera has been distinct from the other neuropteroid lines for a very long time.

The postulated composite patterns and the changes in them that are needed for the differentiation of the other more primitive neuropteroid groups may be determined by comparing tables 2 and 3, and do not require special comment except to note that, compared with the orthopteroid series, relatively large changes, involving several muscles, are usually necessary.

As stated on page 142, the Trichoptera and Lepidoptera could be derived directly from the Megaloptera or Coleoptera; whereas the present Neuroptera, through their loss of *Isps-fu₂* which the Trichoptera and Lepidoptera still retain, can no longer stand in the direct line of descent of these two groups. If, as most authorities agree, the Trichoptera are offshoots of the neuropteroid stock, they must therefore have branched from it at a time before the differentiation of the Neuroptera from the Coleoptera. So far as their limited spinasternal musculature is concerned, there is nothing in either order to prevent derivation of the Lepidoptera from the same line that gave rise to the Trichoptera. The numerous other possible derivations of the two orders that the spinasternal musculature would permit may be dismissed as probably of no genetic significance.

The Hymenoptera, though they have only five spinasternal muscles, have, like the Mecoptera, preserved *Icv-cx₁X*. If they are to be traced to a neuropteroid source, they must be associated with a group that had retained this muscle after its disappearance from the lines that led to the Megaloptera, Coleoptera, and Neuroptera. The Hymenoptera possess two spinasternal muscles that the Mecoptera lack, if one accepts Weber's (1927) interpretation of the muscles of tenthredinids, and could therefore be continued in close association with the mecopteran line only down to the point where it lost *Isps-cx₁* and *2sps-fu₃*. The present Mecoptera also show the muscle *Isps-fu₁* in the form *fu₁-fu₁*, a specialization that has not been reported for any hymenopterous species. As noted on page 142, the spinasternal musculature of Hymenoptera is also derivable from orthopteroid sources; and it offers us no facts that would permit a decision as to their true affinities.

We may mention here that the larval musculature of Trichoptera, Lepidoptera, brachycerous Diptera, and Hymenoptera, and of most beetles, does not include spinasternal muscles, so that it contributes nothing to the problem with which we are here concerned. Spinasternal muscles are present, however, in the larvae of the other holometabolous orders that have been examined; and in the nymphs of most Hemimetabola. Culicid larvae also are said to have transverse muscles that may be remnants of a spinasternal musculature.

The Odonata, which like the Dermaptera have nine spinasternal muscles, hold a somewhat anomalous position; and that they have long been separate from the rest of the Pterygota is as evident in their spinasternal musculature as in other facets of their organization. If our interpretation of the reported data is correct, the dragonflies possess the muscle *2sps-3ils*, which is found elsewhere only in Thysanura, Megaloptera, and Coleoptera; yet the Odonata have also *1cv-cx₁X*, which the beetles and dobsonflies lack. Since the presence of *1cv-cx₁X* in the Mecoptera suggests that this muscle was distributed among primitive neuropteroids before the Megaloptera and Coleoptera became separated from them, the Odonata, as far as their spinasternal muscles are concerned, could have come from this same basic neuropteroid stem. But the Odonata could equally well be traced to an orthopteroid origin, since many present orthopteroids possess *1cv-cx₁X*; while, as we have seen, the immediate ancestors of these orthopteroid forms must have had a *2sps-3ils* that had not yet disappeared nor been converted into the *2sps-1ils* of some existing orthopteroid species. We have mentioned on page 141 that a derivation of the odonatan pattern directly from one like that of the Thysanura is likewise possible. Our evidence thus leaves several choices, whose common feature is merely that they all place the separation of the Odonata from the other Pterygota well back in time. Simultaneously, the facts afford proof that the Odonata share a distant common ancestry with other winged insects; but more than this they do not tell us.

The Mallophaga, too, present difficulties; for their possession of *1cv-cx₁X* among a total of six spinasternal muscles tends to cast them either with the orthopteroid orders or with some offshoot of the postulated primitive neuropteroid line, while their ownership of *3sps-3ils* is not paralleled in any existing orthopteroid group. On either alternative, the direct line of their descent would seem to go far back, and their affinities to psocopteroid insects would therefore appear less close than some students of other criteria have thought.

Also unexpected is the high degree of similarity between the Mallophaga and the phasmids. Not only do the Mallophaga possess all four of the spinasternal muscles that have been found in the walkingsticks, but they possess them with similar modifications. The resemblances extend further than the musculature, to the relative proportions of the three thoracic segments, the odd position of each coxa within its segment, and the unusual form of the respective segmental sternal apophyses. The Phasmatodea are of course ordinarily placed

with the orthopteroid groups, but their possession of *3sps-3ils* (as *3ils-3ils*) raises the same obstacle that we have just confronted in discussion of the biting lice. Thus, the position of the Mallophaga and Phasmatodea remains uncertain. One may note in passing that several of the structural peculiarities of these two orders are shared by the Mecoptera.

Direct derivation of the Embiodea from the Orthoptera or Psocoptera (p. 142) overlooks the fact that the Embiodea have been reported (Maki, 1938, fig. 16, No. 9) to have an anomalous furcal muscle inserted on the prosternum between the nerve cords, anterior to the normal *1sps-fu₁*, which is present. Apparently there are also other anomalies in the ventral body musculature of the Embiodea, and their true affinities will not be clarified until the nature of these peculiar muscles has been resolved. Meanwhile, it seems most probable that the Embiodea are offshoots of the orthopteroid stem somewhere in the vicinity indicated on page 143.

The spinasternal musculature of the remaining orders that have been suitably studied, namely Ephemeroptera, Thysanoptera, Homoptera, Hemiptera, and Diptera, is not such as to permit further inferences as to the relationships of these groups.

CONCLUSION

The conclusions that we have been able to reach, on the basis of the spinasternal musculature, are given for the orthopteroid and neuropteroid orders in table 3. In figure 1, some groups of more doubtful affinity are included, in positions that reflect what seem the most likely among the various possibilities for their derivation. Since our judgment still rests on rather scanty data for a number of orders, we have been concerned primarily to suggest the sort of analysis that a really thorough comparative study of the musculature of insects would permit; in this sense, we should like to regard our present conclusions as a beginning rather than an end.

TABLE 3.—*Probable pathways of evolution of the spinasternal muscles in certain orthopteroid and neuropteroid orders*

1. Prethysanura (28 muscles; see table 2)	
Less <i>2sps-cps₂</i> ; convert to ligaments <i>1sps-fu₁</i> , <i>2sps-fu₂</i> , <i>3sps-fu₃</i> , <i>1sps-1ils</i> , <i>2sps-2ils</i> , <i>3sps-3ils</i> , <i>1sps-cps₂</i> ; convert <i>2sps-1ils</i> , <i>3sps-2ils</i> , <i>1sps-3ils</i> to <i>2sps-pl₁</i> , <i>3sps-pl₂</i> , <i>1sps-pl₃</i> , respectively.....Thysanura	
Less <i>1sps-3ils</i>	Prepterygota (2)
2. Prepterygota	
Less <i>1sps-2sps</i> , <i>2sps-3sps</i> , <i>3sps-1sps</i>	Preneuropteroids (10)
Less <i>2sps-1ils</i> , <i>3sps-s₁</i> , <i>3sps-2ils</i> , <i>3sps-fu₂</i>	Preorthopteroids (3)

(Continued)

TABLE 3.—(Continued)

3. Preorthopteroids
 - Less *1sps-2ils*, *3sps-3ils*; convert *2sps-3ils* to *2sps-lils*
 - Blattoid-Orthopteroid-Pscopteroid composite (4)
4. Blattoid-Orthopteroid-Pscopteroid composite
 - Less *2sps-fu₂*Preblattids (5)
 - Less *2sps-lils*, *2sps-3sps*, *3sps-1sps*, *3sps-cx₃*
 - Orthopteroid-Pscopteroid composite (8)
5. Preblattids
 - Modify *3sps-cx₃* to *fu₃-cx₃*.....Blattariae
 - Less *1sps-2sps*, *3sps-1sps*
 - Isoptera-Grylloblattodea-Mantodea composite (6)
6. Isoptera-Grylloblattodea-Mantodea composite
 - Less *2sps-lils*, *2sps-lils*, *2sps-3sps*, *1cv-cx₁X*.....Isoptera
 - Less *1sps-cx₁*.....Mantodea-Grylloblattodea composite (7)
7. Mantodea-Grylloblattodea composite
 - Less *1sps-fu₁*, *2sps-2ils*, *2sps-cx₃*, *2sps-lils*, *2sps-fu₁*.....Mantodea
 - Less *1sps-cps₂*, *2sps-cx₂*, *2sps-3sps*, *3sps-fu₁*, *3sps-lils*.....Grylloblattodea
8. Orthopteroid-Pscopteroid composite
 - Less *1sps-lils*Orthoptera
 - Less *1sps-cps₂*, *2sps-cx₂*.....Pscoptera-Plecoptera complex (9)
9. Pscoptera-Plecoptera complex
 - Less *2sps-2ils*Pscoptera
 - Less *1sps-2sps*, *2sps-fu₂*, *2sps-cps₂*, *3sps-fu₁*, *3sps-lils*.....Plecoptera
10. Preneuropteroids
 - Less *1cv-cx₁X*.....Megalopteroid-Coleopteroid complex (11)
 - Less *1sps-cx₁*, *1sps-cps₂*, *1sps-cx₂*, *1sps-2ils*, *1sps-fu₂*, *2sps-cx₂*, *2sps-2ils*, *2sps-cps₂*, *2sps-cx₃*, *2sps-3ils*, *2sps-lils*, *2sps-fu₁*, *3sps-cx₃*, *3sps-lils*, *3sps-s₁*, *3sps-2ils*, *3sps-fu₂*.....Mecoptera
11. Megalopteroid-Coleopteroid complex
 - Less *1sps-2ils*, *2sps-fu₂*, *3sps-2ils*, *3sps-fu₂*.....Megaloptera
 - Less *1sps-cps₂*, *2sps-cps₂*, *2sps-fu₁*, *3sps-lils*, *3sps-s₁*
 - Coleoptera-Neuroptera complex (12)
12. Coleoptera-Neuroptera complex
 - Less *2sps-fu₂*, *3sps-fu₃*Coleoptera
 - Less *1sps-cx₂*, *1sps-fu₁*, *2sps-2ils*, *2sps-3ils*, *3sps-cx₃*, *3sps-3ils*, *3sps-2ils*, *3sps-fu₂*Neuroptera

SUMMARY

Comparison of the spinasternal musculature of the Thysanura and 24 orders of pterygote insects leads to the following conclusions in regard to their relationships:

1. The Thysanura are close to the ancestral pattern, but not in the direct line of pterygote descent.

2. The Pterygota may be divided naturally into two large series that include the orthopteroid and neuropteroid orders respectively, plus a number of orders of uncertain position.

3. The orthopteroid series includes the Blattariae, Isoptera, Man-

todea, Grylloblattodea, Orthoptera, Psocoptera, and Plecoptera. The Dermaptera also are possibly orthopteroid; but in any case they have probably had a long independent existence.

4. The neuropteroid series includes the Megaloptera, Coleoptera, and Neuroptera, and probably the Trichoptera and Lepidoptera. If the Mecoptera belong here, they were separated from the other orders named at an early date.

5. The relationships of the Hymenoptera are quite uncertain.

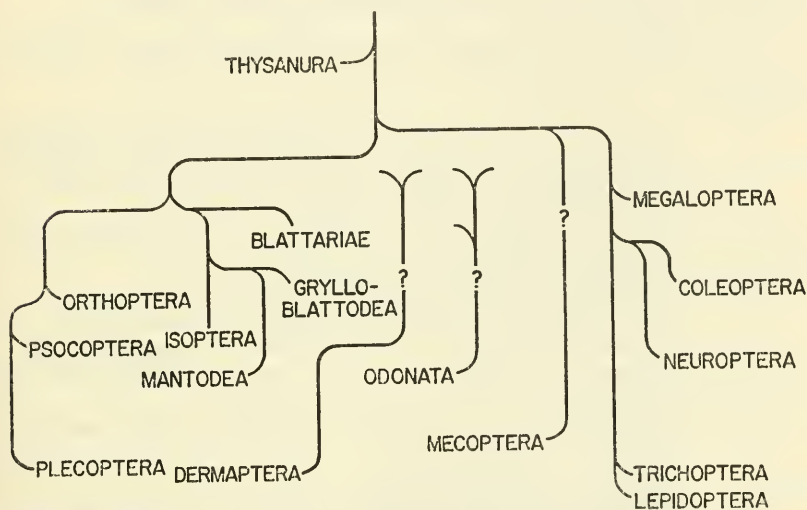


FIG. 1.—The apparent relationships of some orders of insects, as seen in their spinasternal musculature. Uncertain affinities, for which there is some evidence, are indicated by question marks. Available data do not permit even tentative placement of the Mallophaga, Phasmatodea, Embiodea, Ephemeroptera, Thysanoptera, and Homoptera, which are known to possess a few spinasternal muscles.

6. The Odonata have been separated from the other Pterygota for a very long time. Their spinasternal musculature indicates an early derivation for them, but does not permit a choice among several possibilities.

7. Also difficult to place are the Mallophaga and Phasmatodea. Conventional derivations for these two orders appear to conflict with the facts revealed in their spinasternal musculature, but the latter is too reduced to serve as a guide to definite placement.

8. The spinasternal muscles of the remaining orders that have been studied are not informative as to the affinities of these groups. These include the Embiodea, Ephemeroptera, Thysanoptera, Homoptera,

Hemiptera, and Diptera. Adult Coleoptera would be placed here also, except that we know that they must be descendants of the same stock that produces their larvae.

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THE NERVES AND MUSCLES OF THE PROBOSCIS OF THE BLOW FLY *PHORMIA REGINA* MEIGEN IN RELATION TO FEEDING RESPONSES¹

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INTRODUCTION

To say that structure and function are inseparable is almost tautological; nevertheless, in the early history of biology, and until very recent times in entomology, structure has commonly been studied for the sake of structure. Developmental morphologists and students of phylogeny have approached the study of structure from a dynamic point of view, but few entomological anatomists have come to the subject with the thought of function uppermost in their minds. Not infrequently it falls to the lot of the physiologist probing the functional mysteries of some insect to survey and map his own anatomical route. With the increased use of electrophysiological techniques by the physiologist the need to know the pathways of various nerves, which trunks contain afferent fibers and which efferent, the identity of muscle innervation, the relations of various fibers to ganglia and to the endocrine system, and where to place electrodes has, with other needs of a similar nature, become urgent. The study of finer structure has thus taken on a new aspect engendered by recent advances in insect physiology. The study of chemoreception in the blow fly *Phormia regina* Meigen is a case in point.

Since the first quarter of the century when Minnich (1922) demonstrated that adult Lepidoptera respond to appropriate chemical stimulation of the tarsi and mouth parts by extending the proboscis, the proboscis response has been exploited by many investigators, notably, Minnich himself (1922 to 1931), Frings (1946), Frings and O'Neal (1946), Haslinger (1935), Dethier and Chadwick (1947), and Dethier (1957) as a means of conducting quantitative physiological and behavioral studies of the chemical senses. Grabowski and Dethier (1954) and Dethier (1955) showed that it was possible to elicit a complete behavioral response, that is, complete extension of the pro-

¹ This work was aided by a grant from the National Science Foundation.

boscis, by stimulating single chemoreceptive hairs on the tarsus or labellum of the blow fly. Following the development by Hodgson, Lettvin, and Roeder (1955) of means of recording electrically from single hairs, several workers have begun detailed correlative studies of the behavioral and electrophysiological events incorporated in proboscis extension, the first component act of the feeding reaction. Great interest attaches, therefore, to the precise route which the action potentials generated in the chemoreceptor unit follow to and through the cerebral ganglia and thence to the effectors which cause the proboscis to extend. Similarly, there is interest in the pathways utilized by action potentials generated by unacceptable compounds, such as sodium chloride, which are rejected by the fly and result in withdrawal of the proboscis. It becomes necessary, therefore, to map the course of the nerves in the head and the origins and insertions of the various muscles associated with movements of the proboscis.

The most complete morphological studies of the proboscis of muscoid Diptera have been those of Lowne (1870, 1890-95) on *Calliphora vomitoria* and *C. erythrocephala*, Hewitt (1914) on *Musca domestica*, Graham-Smith (1930) on *Calliphora erythrocephala*, and Snodgrass on a variety of species. Although *Phormia regina* has been the subject of numerous physiological studies, it has not attracted the attention of morphologists. The present study was undertaken with the views peculiar to physiology foremost in mind.

METHODS

Dissections were made on freshly killed flies which were from 2 to 5 days old and on specimens preserved in alcoholic Bouin's fixative. When fresh specimens were employed, the tissues were first bathed in a methylene blue solution which was then drained off and replaced with water. In addition to gross dissection, serial sections were prepared by the usual histological techniques.

THE FEEDING REACTION

The feeding reaction of the blow fly as described by Dethier (1955) and Dethier, Evans, and Rhoades (1956) may be subdivided into the following component actions: Extension of the proboscis, spreading of the labellar lobes, and sucking. The complete sequence of events may be brought about by stimulation of a single labellar or tarsal chemoreceptive hair. Although each hair is provided with three bipolar neurons, evidence from electrophysiological studies has shown that only one need be activated for proboscis extension. Sucking

may also be initiated by stimulation of interpseudotracheal papillae, and it is probable that here also stimulation of a single cell may suffice.

Feeding may be terminated as a result of: (1) cessation of sensory input from the cells mentioned either by removal of the stimulus or by adaptation; (2) central adaptation; (3) inhibitory impulses into the brain from the gut, signaling satiation (Dethier and Bodenstern, 1958); (4) stimulation of rejection neurons in the chemoreceptive hairs of the tarsi or labellum.

The fact that many phases of the complicated feeding response may be triggered by a single cell raises the interesting question of how the afferent impulses are routed once they reach the brain. Furthermore, it is of interest that the sequence of events is ordered, that the number of steps, the simultaneity of steps, and even the omission of steps under certain experimental conditions all follow from stimulation of a single neuron and are controlled apparently by the frequency of afferent impulses which in turn are regulated by the intensity of the stimulus.

In addition to the simple situation as just outlined, there are more complicated experimental situations where antagonistic stimuli may be balanced, with the result that the feeding response which is elicited may be complete acceptance, complete rejection, or some intermediate action.

Eventually the analysis of neural pathways will have to be made electrophysiologically; nevertheless, as a preliminary step, it is desirable to learn which effectors are employed in the above-mentioned situation and what their innervation may be.

MUSCLES OF THE PROBOSCIS

The proboscis of the blow fly is a tubular erectile organ evolved from the mouth parts and clypeal regions of the head (fig. 1). In repose it lies withdrawn into the ventral regions of the head capsule. It consists of three well-defined sections; the proximal section or rostrum, the middle section or haustellum, and the distal oral disc. The principal supporting element is a large internal skeletal piece termed the fulcrum.

There are 16 muscles in the proboscis of the blow fly; 5 have their origins in the head capsule, 7 originate in the rostrum, and 4 originate in the haustellum.

The muscles of the proboscis of *Phormia* are nearly identical to those of *Calliphora* as described by Graham-Smith (1930); accordingly, his nomenclature and scheme of presentation will be employed in the following detailed descriptions.

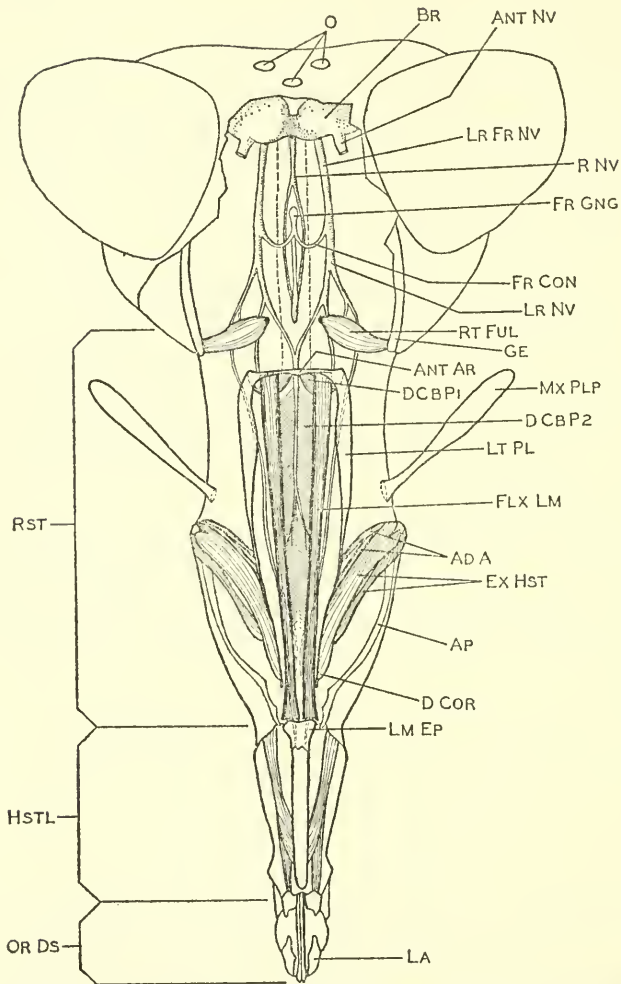


FIG. 1.—Muscles and labrofrontal innervation of the proboscis of *Phormia regina* Meigen, anterior aspect.

Rst, rostrum; *Hstl*, haustellum; *OrDs*, oral disc; *O*, ocelli; *Br*, brain; *AntNv*, antennal nerve; *LrFrNv*, labrofrontal nerve; *RNv*, recurrent nerve; *FrGng*, frontal ganglion; *FrCon*, frontal ganglion connective; *LrNv*, labral nerve; *RtFul*, retractor of fulcrum; *Ge*, gena; *AntAr*, anterior arch of fulcrum; *DCbP₁*, *DCbP₂*, dilators of cibarial pump; *MxPlp*, maxillary palpus; *LtPl*, lateral plate of fulcrum; *FlxLm*, flexor of labrum; *AdA*, adductors of apodeme; *ExHst*, extensors of haustellum; *Ap*, apodeme; *DCor*, distal cornu of fulcrum; *LmEp*, labrum-epipharynx; *La*, labellum.

MUSCLES ORIGINATING IN THE HEAD CAPSULE

Retractors of the fulcrum (figs. 1, 3, *RtFul*).—These are short, robust muscles originating on the internal anterior edges of the genae. They are inserted into the extremities of the posterior cornua of the

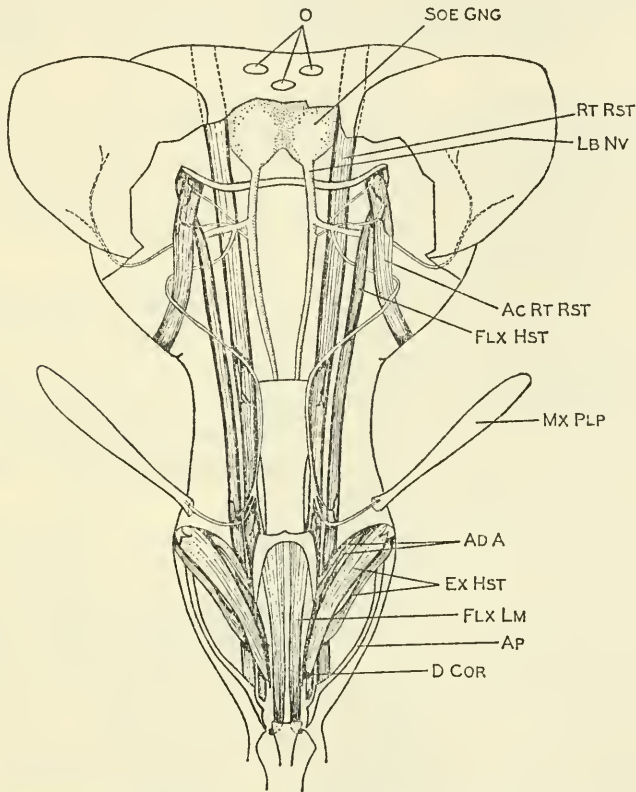


FIG. 2.—Muscles and labial innervation of the proboscis of *Phormia regina* Meigen, anterior aspect.

O, ocelli; *SoeGng*, subocsofageal ganglion; *RtRst*, retractor of rostrum; *LbNv*, labial nerve; *AcRtRst*, accessory retractor of rostrum; *FlxHst*, flexor of haustellum; *MxPlp*, maxillary palpus; *AdA*, adductors of apodeme; *ExHst*, extensors of haustellum; *FlxLm*, flexor of labrum; *Ap*, apodeme; *DCor*, distal cornu of fulcrum.

fulcrum. As described by Lowne (1892) and Graham-Smith (1930), their contraction causes the lower end of the fulcrum, i.e., the region of the distal cornua, to describe a circular arc so that the fulcrum is retracted to a horizontal position between the genae. These muscles are innervated by fibers from the lateral branches of the labral nerve.

Retractors of the rostrum (figs. 2, 3, *RtRst*).—These are the

longest muscles of the proboscis. They originate from the dorsolateral regions of the occiput and are inserted into the sesamoid sclerite, the ventral surface of the hypoglossa near the proximal ends of the paraphyses, and the distal extremity of the mentum. By their contraction the entire proboscis is retracted. They are innervated at several points along their length by fibers from the lateral branches of the labial nerve.

Accessory retractors of the rostrum (fig. 2, *AcRtRst*).—The origins of these muscles and the next are the sides of the occipital foramen. They are inserted into the ventral integument of the rostrum close to the head capsule. Their contraction assists in the retraction of the entire proboscis. They are innervated by small fibers from both branches of the labial nerve.

Flexors of the haustellum (figs. 2, 3, *FlxHst*).—These slender muscles, the second longest in the proboscis, originate at the sides of the occipital foramen laterad of the accessory retractors of the rostrum and pass behind these, whence they extend to flexures of the apodemes of the labrum. By their contraction they flex the haustellum on the anterior face of the rostrum. They are innervated principally by fibers from the lateral branches of the labial nerve.

Retractors of the oesophagus (figs. 3, 6, *RtOes*).—Graham-Smith and Lowne described "small bundles of muscle fibers which arise from the lower part of the frontal sac, or remains of the ptilinum, and which are inserted into the muscular coat of the oesophagus between the fulcrum and the brain. . . . They serve to draw the loop of the oesophagus, which lies between the cephalic ganglia and the fulcrum, forward, when the proboscis is retracted into the head capsule." If these muscles occur in *Phormia*, they are most inconspicuous. The loop of the oesophagus, as well as the loops of the frontal connectives and the frontal ganglion, are suspended by a network of fine tracheae and fat body extending to the region of the frons and ptilinum.

There is, however, on each side a fine but conspicuous muscle consisting of two strands of fibers, which originates in the integument between the antennal sockets, extends posteriorly, and in the company of the oesophagus and the recurrent nerve passes through the opening which separates the brain and the suboesophageal ganglion. The fibers are inserted into the muscular coat of the wall of the oesophagus posterior to the brain. It is possible that these delicate muscles may be the retractors of the oesophagus; however, since they apparently pull the oesophagus forward they may more aptly be termed protractors.

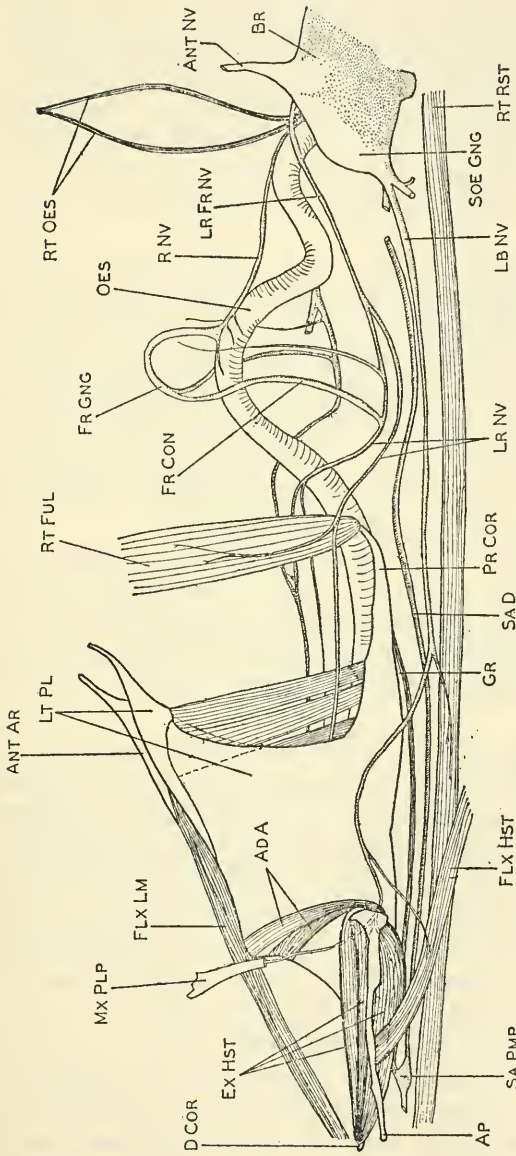


FIG. 3.—Muscles and innervation of the rostrum of *Phormia regina* Meigen, lateral aspect.

AdA, adductors of apodeme; *AntAr*, anterior arch of fulcrum; *AntNv*, antennal nerve; *Ap*, apodeme; *Br*, brain; *DCor*, distal cornu of fulcrum; *ExHst*, extensors of haustellum; *FlxLm*, flexor of labrum; *FlxHst*, flexor of haustellum; *FrCon*, frontal ganglion connective; *FrGng*, frontal ganglion; *Gr*, gracilis muscle; *LbNv*, labial nerve; *LxFrNv*, labrofrontal nerve; *LxNv*, labral nerve; *LtPl*, labral plate of fulcrum; *MxPlp*, maxillary palpus; *Oes*, oesophagus; *PrCor*, proximal cornu of fulcrum; *RNV*, recurrent nerve; *RtFul*, retractor of fulcrum; *RtOes*, retractors of oesophagus; *RtRst*, retractor of rostrum; *SaD*, salivary duct; *SaPmp*, salivary pump; *SoeGng*, suboesophageal ganglion.

MUSCLES ORIGINATING IN THE ROSTRUM

Extensors of the haustellum (figs. 1, 2, 3 *ExHst*).—Three distinct bundles of fibers comprise this short, stout muscle which originates on the distal cornua and adjacent regions of the fulcrum and is inserted into the outer sides of the heads of the apodemes. When these muscles contract, they force the apodemes downward away from the head and cause the haustellum to extend. They are innervated by small branches leaving the labial nerve in the region of the nerve of the palpus.

Adductors of the apodemes (figs. 1, 2, 3, *AdA*).—These muscles, consisting of two bundles each, originate on the anterior distal margins of the lateral plates of the fulcrum. They are inserted into the inner sides of the heads of the apodemes. By their contraction they draw the heads of the apodemes toward the median line. In so doing they cause the haustellum to be extended. Thus, together with the extensors of the haustellum, they work to extend this section of the proboscis. The nerves serving these muscles are small fibers leaving the labial nerve in the region of the branch to the palpus.

Flexors of the labrum (figs. 1, 2, 3, *FlxLm*).—These long, flat muscles have their origins on the distal edge of the anterior arch of the fulcrum and from the adjacent areas of the lateral plates. They are inserted into the sides of the lateral cornua of the labrum in close proximity to the articulations of the apodemes. They are innervated by the labral nerve.

Gracilis muscles (fig. 3, *Gr*).—These thin, delicate muscles have their origins at the bases of the proximal cornua of the fulcrum. They are inserted into the anterior wall of the salivary pump. They control the flow of saliva into the salivary canal of the hypopharynx.

Dilators of the cibarial pump (fig. 1, *DCbP₂*).—According to Graham-Smith these powerful muscles (which he termed pharyngeal muscles) arise from the internal surfaces of the anterior arch and lateral plates of the fulcrum. In *Phormia* there appear to be three distinct sets of muscles. Two of these (*DCbP₁*) originate at a flexure in the outside surface of the lateral plate in the region of the anterior arch. The remaining massive muscle originates on the internal surfaces of the anterior arch and lateral plates. All are inserted into the dorsal plate of the oesophagus. These are the muscles the action of which pumps fluid into the oesophagus. They act by drawing the dorsal plate of the oesophagus away from the ventral plate of the fulcrum. They are innervated by both branches of the labrofrontal nerve.

Epipharyngeal muscles.—These small muscles in *Phormia* are similar to their counterparts in *Calliphora*. They originate on the “handle” of the hypopharynx and free portion of the salivary canal and are inserted into the adjacent walls of air sacs of the rostrum as well as on neighboring integument. As Graham-Smith surmises, they assist in disposition of parts during flexion and extension.

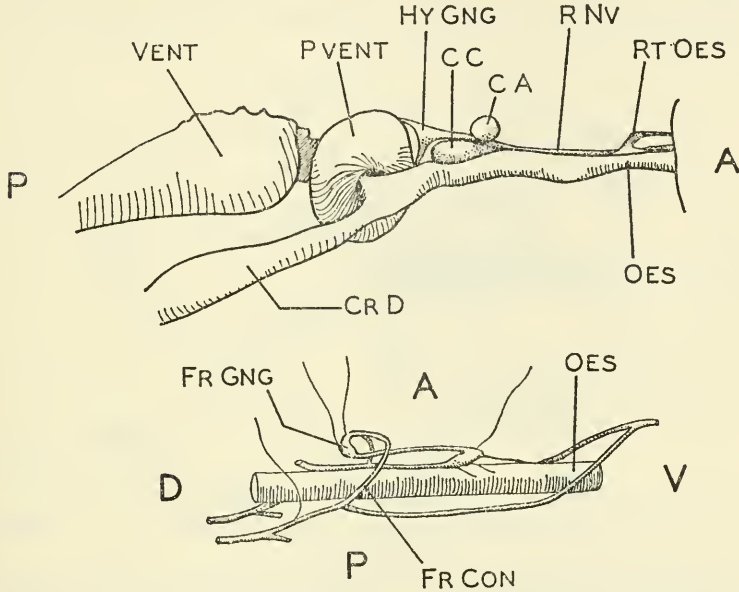


FIG. 4.—Upper: Detail to show relation of insertion of the retractors of the oesophagus to the recurrent nerve, lateral aspect. Lower: Detail of frontal ganglion and its connectives, lateral aspect.

CA, corpus allatum; *CC*, corpus cardiacum; *FrCon*, frontal ganglion connective; *FrGng*, frontal ganglion; *HyGng*, hypocerebral ganglion; *Oes*, oesophagus; *Pvent*, proventriculus; *RNV*, recurrent nerve; *RtOes*, retractors of oesophagus; *Vent*, ventriculus.

A, anterior; *P*, posterior; *D*, dorsal; *V*, ventral.

MUSCLES ARISING IN THE HAUSTELLUM

Retractors of the furca (fig. 5, *RtFur*).—These muscles arise on the inner lateral surfaces of the mentum and are inserted into tubercles on the lateral processes of the furca. Their action has been described in detail by Graham-Smith. “Contraction of these muscles causes the lateral processes, carrying the labella with them, to rotate outwards on the mento-furcal bars. Further contraction causes progressive folding back of the labella.” Innervation is by fibers from the labial nerve.

Transverse muscles of the haustellum (fig. 5, *TrHst*).—These originate near the midline of the internal surface of the mentum and are inserted on the paraphyses. They assist in extending the oral disc by shortening the paraphyses. They are innervated by branches of the labial nerve.

Dilators of the labrum-epipharynx.—These are short muscles originating on the internal surface of the labrum and inserting into the outer surface of the epipharynx. Presumably they cause alteration

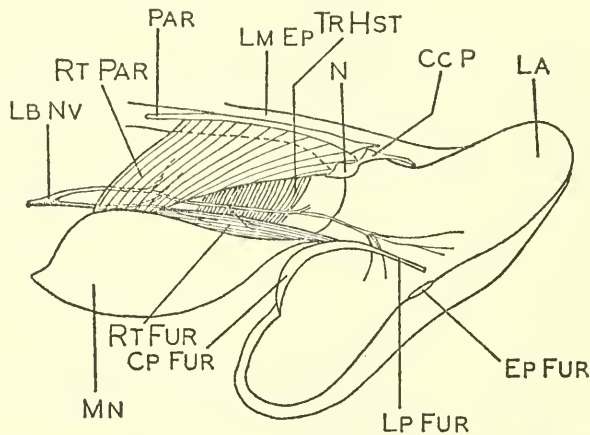


FIG. 5.—Muscles and innervation of the oral disc of *Phormia regina* Meigen, lateral aspect.

CcP, cochleariform process; *CpFur*, central process of furca; *EpFur*, epifurca; *La*, labellum; *LbNv*, labial nerve; *LmEp*, labrum-epipharynx; *LpFur*, lateral process of furca; *Mn*, mentum; *N*, nodulus; *Par*, paraphysis; *RtFur*, retractor of furca; *RtPar*, retractor of paraphysis; *TrHst*, transverse muscle of haustellum.

of the diameter of the epipharyngeal cavity (Graham-Smith). They are innervated by fibers from the labral nerve.

INNERVATION OF THE PROBOSCIS

The most conspicuous nerves leading from the brain are the paired antennal nerves, the so-called median ocellar nerve, and the paired labrofrontal nerves. The large paired labial nerves connect with the suboesophageal ganglion. The proboscis is innervated entirely by the labrofrontal and the labial nerves.

Labrofrontal nerves (figs. 1, 3 *LrFrNv*).—The labrofrontal nerves extend from the brain from positions slightly ventrad and mesad of

the antennal nerves. They are smaller in diameter than the antennal nerves. They pass down the proboscis on either side of the oesophagus. Each one shortly branches. The branch nearer the midline divides again, and part of it curves anteriorly and dorsally meeting the corresponding branch of the opposite side and uniting with it in a single nerve. This nerve loops to continue ventrally for a short distance along the oesophagus before looping once again to reverse its direction and continue dorsally and posteriorly up the oesophagus as the recurrent nerve (figs. 3, 4). The recurving branches are the frontal connectives. In some specimens the frontal connectives leave the main trunk before it branches (fig. 1). The exact disposition of the loops varies depending on whether the proboscis is retracted or extended; however, the first recurved dorsal loop is constant even though its tightness varies. It is suspended from the anterior walls of the proboscis and the anterodorsal wall of the head capsule in the region of the remnants of the pilinum by strands of fine tracheae and fat body, both of which by their elasticity permit great flexibility and shock-absorption of the nerves as the mouth parts move. The most ventral extension of the nerve, before it retraces its dorsal course, gives rise to a small nerve which continues for a short distance down the oesophagus (fig. 4). It also gives off to the surface of the oesophagus at least two lateral pairs of very fine nerves.

The exact position of the frontal ganglion is difficult to ascertain because it is not conspicuously ganglionlike in appearance. After the two frontal connectives fuse, there is a swelling in the region of the first loop and another in the region of the second loop. It is probable that the first is the frontal ganglion.

The recurrent nerve continues along the anterior surface of the oesophagus as it traverses the brain (fig. 3). Emerging posteriorly from the brain, it proceeds along the dorsal surface of the oesophagus and joins the hypocerebral ganglion just anterior to the junction of the crop and proventriculus (figs. 4, 6). Here small nerves branch to the corpus allatum and corpus cardiacum. The largest nerves from the hypocerebral ganglion extend to the crop and to the proventriculus.

After the frontal connectives branch from the labrofrontal nerves, the two medial nerves unite on the anterior surface of the oesophagus in the region of the insertions of the retractors of the fulcrum. The fused nerve then extends down the proboscis passing between the paired dilators of the cibarial pump to which small branches are sent.

The lateral branches of the labrofrontal nerves pass ventrally on either side of the oesophagus, each giving a branch to the retractors of

the fulcrum, passing laterad of these muscles, entering the fulcrum, and extending to the labrum. These extensions constitute the innervation of the labrum-epipharynx.

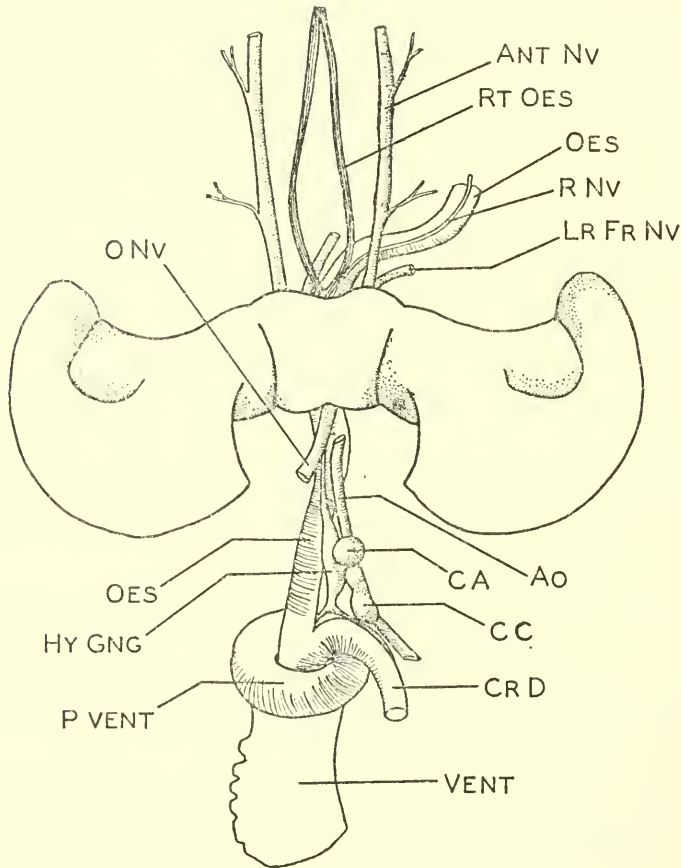


FIG. 6.—Dorsal view of the brain and its nerves.

AntNv, antennal nerve; *RtOes*, retractors of oesophagus; *Oes*, oesophagus; *RNv*, recurrent nerve; *LrFrNv*, labrofrontal nerve; *Ao*, aorta; *CA*, corpus allatum; *CC*, corpus cardiacum; *CrD*, crop duct; *Vent*, ventriculus; *ONv*, ocellar nerve; *HyGng*, hypocerebral ganglion; *PVent*, proventriculus.

Labial nerves (figs. 2, 3, 5, *LbNv*).—The large paired labial nerves extend from the suboesophageal ganglion. Each immediately divides into two large branches. The medial branch extends ventrally along the posterior portion of the proboscis. Almost immediately it gives off a small branch which, extending laterally and dorsally, innervates

the accessory retractors of the rostrum. The principal branch then continues ventrally to the labellum. It innervates the retractors of the furca, the retractors of the paraphyses, and the transverse muscle of the haustellum. It is the principal sensory trunk from the labellum.

The second principal branch of the labial nerve, the lateral branch, immediately subdivides. The more dorsal branch sends a small twig to the accessory retractors of the rostrum, then continues up into the cranial cavity to the tracheae and fat body.

The remaining branch passes anterior to the retractors of the rostrum, then curves posterior to the flexors of the haustellum and the accessory retractors of the rostrum, thence anterior to all three muscles and ventrally down the proboscis. Near the proximal cornua of the fulcrum it gives off a small branch to the retractors of the rostrum. Shortly thereafter it subdivides to send sensory fibers to the maxillary palpi and motor fibers to the extensors of the haustellum and the adductors of the apodemes. To this point at least the main nerve is demonstrated to be a compound maxillary-labial nerve.

EXTENSION OF THE PROBOSCIS

Available evidence suggests that extension of the rostrum is accomplished by distension of the large air sacs contained within it. Lowne (1892) stated that control of the passage of air from the thoracic cavity is exercised by “. . . a slender rod of chitin in its (the tracheal trunk) anterior wall, which closes the tube by pressing against the jugum. This forms a valve capable of being opened by a small bundle of muscle fibers, which arise from the front edge of the gena; their contraction opens the valve and permits the passage of air from the thoracic cavity into the tracheae of the proboscis.” In *Phormia* extension of the rostrum can be prevented by puncturing the air sacs in question or by ligaturing the neck so that no air can be passed into the head. However, the particular muscular arrangement described by Lowne has not yet been observed and further investigation is necessary. If such muscles exist, it is probable that they derive their innervation from branches of the labial nerve arising close to those which innervate the accessory retractors of the rostrum.

Extension of the more distal portions of the proboscis is accomplished by direct muscular action. The haustellum is extended by contraction of the extensors of the haustellum and the adductors of the apodemes. The oral disc is extended by contraction of the retractors of the paraphyses and the transverse muscles of the haustellum.

The labellar lobes are opened by contraction of the retractors of the furca. Thus, six sets of muscles (if the muscles of the air sacs be included) contract to give full extension of the proboscis. All are innervated by fibers from the labial nerve.

Sucking is accomplished by the action of the dilators of the cibarial pump. These receive their innervation from the labral nerve.

RETRACTION OF THE PROBOSCIS

Retraction of the proboscis within the head capsule is accomplished entirely by direct muscular action. The haustellum is flexed by the flexors of the haustellum and the flexors of the labrum; the fulcrum is brought into a horizontal position between the genae by contraction of the retractors of the fulcrum; the entire proboscis is drawn up into the head by contraction of the retractors of the rostrum and the accessory retractors of the rostrum. Thus, five sets of muscles are concerned with retraction of the proboscis. All but two of these receive their motor fibers from the labial nerve. The retractors of the fulcrum and the flexors of the labrum receive their motor fibers from the labral nerve.

Closing of the labellar lobes is brought about by elastic recoil when the muscles responsible for extension are relaxed. Cessation of sucking is brought about by relaxation of the dilators of the cibarial pump.

THE FEEDING RESPONSE

A sufficiently intense stimulus, as, for example, 2M sucrose, applied to a single sensory neuron of the labellum can cause vigorous and complete extension of the proboscis. This means that impulses ascend afferent fibers of the labial nerve to the suboesophageal ganglion where they are distributed to a minimum of six different sets of ipsilateral motor fibers and also cross over to six different sets of contralateral fibers. Similarly, stimulation of a single sensory neuron on any of the legs causes impulses to ascend from the thoracic ganglion to the suboesophageal ganglion where the same motor fibers as before are stimulated.

When the intensity of the stimulus is low, there may be only partial extension of the proboscis. This may take the form of extension of the rostrum and partial extension of the haustellum, with the labellar lobes remaining appressed. This reaction would suggest that only fibers to three sets of muscles are affected; namely, the extensors of the haustellum, the adductors of the apodemes, and the indirect mus-

cles controlling extension of the rostrum. On the other hand, under certain conditions, a weak stimulus can cause extension of the haustellum and spreading of the lobes of the labellum even though the proboscis as a whole is in the retracted position. Under these conditions, three different sets of muscles are receiving adequate stimulation; namely, the retractors of the paraphyses, the transverse muscles of the haustellum, and the retractors of the furca.

It would appear from these observations that the quantitative recruitment of motor fibers is regulated in part by the intensity of sensory input but that information from another source recruits the association neurons responsible for selecting which sets of muscles are to be placed in operation.

Still another type of proboscis response characteristic of a weak stimulus is a leisurely extension which is in marked contrast to the violent extension occasioned by a strong stimulus. It is clear, therefore, that the intensity of stimulus controls not only the recruitment of motor fibers but also the intensity of motor response.

Sucking is carried out in its entirety by the dilators of the cibarial pump. It is initiated by stimulation of either the labellar hairs or the interpseudotracheal papillae and is undoubtedly monitored by sensilla situated in the labrum-epipharynx hypopharynx. The sensilla in the labial and pharyngeal regions send fibers into the labral nerve which, as the labrofrontal nerve, enters the brain. The fibers of the interpseudotracheal papillae and labellar hairs ascend in the labial nerve.

The muscles responsible for sucking are innervated by fibers of the labral nerve. Accordingly, while it is possible that all the fiber tracts utilized for proboscis extension lie within the suboesophageal ganglion, the act of sucking requires that afferent impulses pass via the circumoesophageal connectives to the brain. One might speculate that there is tighter central control over sucking than that exercised over extension. From an adaptive point of view tighter control is obviously desirable. Furthermore, unacceptable compounds which may escape detection by the labellar hairs (e.g., l-arabinose, which is acceptable as far as the labellar hairs are concerned but unacceptable as far as the interpseudotracheal papillae are concerned) stimulate rejection neurons in the interpseudotracheal papillae and are routed to the brain to halt sucking. Recent experiments by Arab (in press) show that sensilla in the labrum-epipharynx also monitor sucking. These sensilla send fibers directly to the brain; consequently, at least spatially, very fine control should be possible.

In the absence of sensory input sucking ceases, and the proboscis

is no longer maintained in the extended position. When sensory input becomes inadequate, stimulation to the muscles holding the proboscis in the extended position ceases, these muscles relax, and the proboscis is passively partially retracted. By elastic recoil the labellar lobes close, the haustellum tends to relax against the rostrum, while the rostrum itself no longer remains fully extended. Failure of adequate sensory input may result from adaptation of the chemoreceptors themselves, central adaptation, or inhibition from the stomatogastric nervous system. Dethier and Bodenstern (1958) have shown that satiation in the fly can be equated with carbohydrate in the foregut, that stimulation of unknown receptors there results in impulses passing up the recurrent nerve to the brain where the effects of otherwise adequate sensory input from the proboscis are inhibited.

Sucking may cease as a direct result of impulses from rejection neurons in the labellar hairs, the interpseudotracheal papillae, or the tarsal hairs. Under these circumstances impulses must inhibit centrally the initiation of potentials in the efferents to the dilators of the cibarial pump.

In contrast to the slow relaxation of the proboscis commonly occurring when sensory input fails, the proboscis can be retracted actively with great speed when adverse stimuli are presented to the labellar or tarsal chemoreceptors. Under these circumstances impulses are routed to five sets of retractors and flexors as already described. Present evidence seems to suggest that active retraction partakes more of an all-or-none reaction than does extension; however, further work may reveal that here also there is recruitment of muscles depending upon the intensity of the adverse stimulus.

The situation becomes even more complicated when the fly is presented with mixtures of acceptable and unacceptable compounds. The mixtures may be applied to a single chemoreceptive hair containing acceptance and rejection neurons, or an acceptable compound may be presented to a neuron on the tarsi simultaneously with presentation of an unacceptable compound on a labellar neuron. In either case, the resultant response depends on the nature of the balance obtained in sensory input (cf. Dethier, 1955; Dethier, Evans, and Rhoades, 1956). If sensory input from the acceptance neuron predominates, the proboscis is extended; if sensory input from the rejection neuron predominates, the proboscis is retracted. It is not surprising that a balance involving such widely separated neurons as labellar and tarsal may operate almost as effectively as a balance involving two labellar hairs because, as has been shown, the input from these various sources

is eventually routed to the same effectors. Similarly, the existence of contralateral inhibition (cf. Dethier, 1953) is not too surprising in view of the fact that unilateral sensory stimulation under normal circumstances (as, for example, one labellar hair) brings about very effective bilateral motor activity.

In addition to the balance which is accomplished by central integration, it has recently been demonstrated by electrophysiological methods (Hodgson et al., 1955) that there is a measure of peripheral integration within a single chemoreceptor hair. Stimulation of one neuron of a labellar hair, with sugar for example, affects the nature of the discharge occurring in the other (rejection) neuron. Conversely, stimulation of the rejection neuron affects the nature of the discharge from the acceptance neuron. These findings have recently been confirmed in our laboratory.

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MORPHOLOGY OF THE LARVAL HEAD OF SOME CHIRONOMIDAE (DIPTERA, NEMATOCERA)

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Morphology must be intimate with function.

R. E. SNODGRASS.

INTRODUCTION

The present paper is a continuation of a study of the anatomy of Chironomidae larvae. The first part of the study¹ related to *Chironomus* larvae, their structural and functional relationships, and the morphological interpretation of the structures. In this paper are presented the results as related to Orthocladiinae, Podonominae, and Tanyptinae.

I beg Dr. R. E. Snodgrass to accept this humble contribution as a tribute which I am honored to offer to the worker whose numerous papers have greatly contributed to the development of entomorphology.

Acknowledgments are made to Professor Dr. Hřabě (Brno) for having furnished two preparations in toto of the head of *Protanypus morio* Zett. (e coll. Zavřel), to Miss Marguerite Gouin for the translation into English, and to Miss Helen Sloan for the revision of the text.

ORTHOCLADIAN AND PODONOMIAN STRUCTURES

ORTHOCLADIAN BUCCAL STRUCTURE

The many aquatic and terrestrial species of the subfamily Orthocladiinae (s.l.), are distributed among numerous forms grouped around genera *Orthocladius*, *Diamesa*, *Corynoneura*, and *Clunio* (Goetghebuer, 1932).² We shall choose as a typical form of the structure called "lasiophagous" the very common larva of *Cricotopus* gr. *silvestris* Fabr. (= "*Eucricotopus silvestris*-Gruppe" of Thienemann), "lasiobiotic" species (Meuche), which is characteristic of

¹ To be published by the Société Entomologique de France (in press).

² See note at top of list of references.

the animal associations of standing-water algae, and which feeds on organisms fixed upon the substratum. This structure will later be presented in three modifications realized by species of the genus *Diamesa* frequenting torrents, by *Prodiamesa olivacea* Mg., detritivorous, and by *Protanypus morio* Zett., predaceous, all belonging to the *Diamesa* group.

BUCCAL STRUCTURE OF THE LARVA OF
CRICOTOPUS GR. SILVESTRIS FABR.³

At first sight, this structure, considered as a typical one, appears as a simplification of the chironomian structure pertaining to the labral and epipharyngeal area and to the hypochilum. The setae and dorsal labral chaetae (sensillae I to IV, chaetae, spinulae of Zavřel), placed similarly as in the *Chironomus* larva, are shorter and are moreover very variable from one genus to another. The epipharyngeal area does not have the double pectinate chaeta mentioned by the present writer (1957, p. 111). The other labral-epipharyngeal elements do not present any particular characteristics. The mandible has no dorsal brush, and the inner ventral brush is rather reduced. There is no mesorial brush. Generally, the chaeta and the setae are not divided (except the sensilla III); they consequently are hooks rather than combs.

The most remarkable modifications pertain to the anterior ventral region; in its median part, termed "hypochilum," it is composed, as in *Chironomus*, of the bandlike sclerite doubling the external wall, termed "rabat" by the present writer; it also shows a row of teeth opposed to the mandible. The labium also is constructed as in *Chironomus* and bears setiform and rodlike sense organs and cuticular processes that are extremely abundant and varying. But there are notable differences of structure in the adjacent parts. The submaxillary wall is not double; the striated paralabial plates of *Chironomus* have no equivalent in the Orthocladiinae, and consequently the maxillae are directly inserted on the strengthened subgenal cranial wall (*Sg*) by interposition of the setae-bearing maxillary sclerite (*SMx* 3+4); in front this sclerite is directly continued into the stipes (figs. 1, 3, 5). On the other hand, the hypochilum is strongly

³ For a more detailed description of the mouth parts we refer to Kettisch's (1936-1937) paper on *Cricotopus trifasciatus* P., the larva of which undermines the leaves of *Potamogeton*. This author, too, analyzes the functioning of the mouth parts and emphasizes the prehensile function of the mandible. But in *Cr. cf. silvestris* L. we have not found the tenuous muscle fibers joining the maxillary lobe to the hypopharynx, mentioned by Kettisch (p. 259).

arched, its internal wall is very thick, both walls dorsally and laterally are quite far apart, thus leaving a wide space. So on preparations in toto the hypochilum appears to have small winglike expansions to the right and left of the median part. This conformation of the base of the hypochilum has been recognized by several authors (Pagast, Strenzke, Zavřel, and others) who designate it by different terms such as "Orimente," "Flügelpartieen," "lamina basalis."

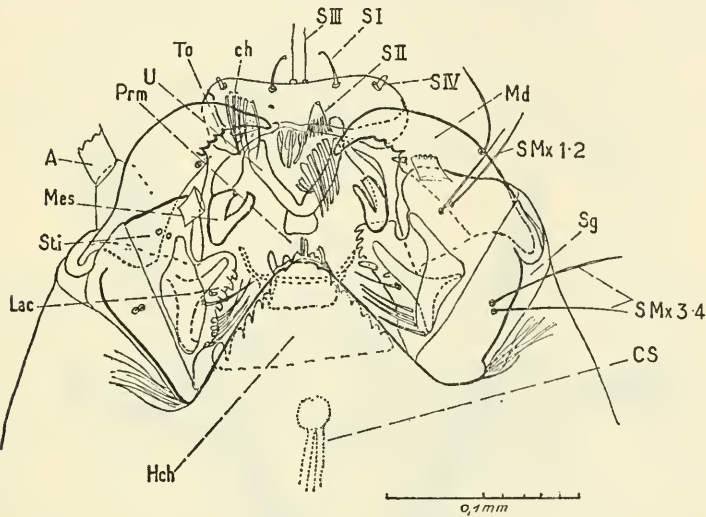


FIG. 1.—*Psectrocladius* cf. *psilopterus* K.

Typical orthocladian structure. Ventral view of the anterior part of the head. The labral chaetae (*ch*) number about a dozen; the lateral hypochilan teeth are supported by the interior wall as in all the other forms. The situation of the salivary duct and pump (*CS*) is indicated by stippling. Cf. figs. 1, 2, and 3 of Gouin (1957), and figs. 3, 5, 6, and 7 of this paper.

These "laminae" are only the lateral parts of the hypochilum and are, moreover, much enlarged. They are therefore not homologous with the chironomian paralabial plates; on this point also the orthocladian structure appears as a simplified chironomian structure.

These buccal organs serve to scrape the surfaces of flints, rocks, branches, etc., whereas the chironomian structure is rather of use in dealing with a soft substratum such as slime or fine particles collected in the tube. This "lasiophagous" structure (Gouin) is present in the numerous species of the subfamily Orthocladiinae (s.l.), species populating the most diverse aquatic habitats as well as some that are terrestrial. One must expect to find numerous variations of this struc-

ture; but comparatively speaking, the variations are very minute, most often concerning the shape and the number of the hypochilan teeth, the shape and the division of the labral chaetae or of the pre-mandible. We cannot here detail these modifications of the buccal organs, which, because of their extreme variability, supply excellent tests for the identification of the genera and even of the species, and are expounded in every work of identification (cf. Goetghebuer 1932, Thienemann 1944).⁴

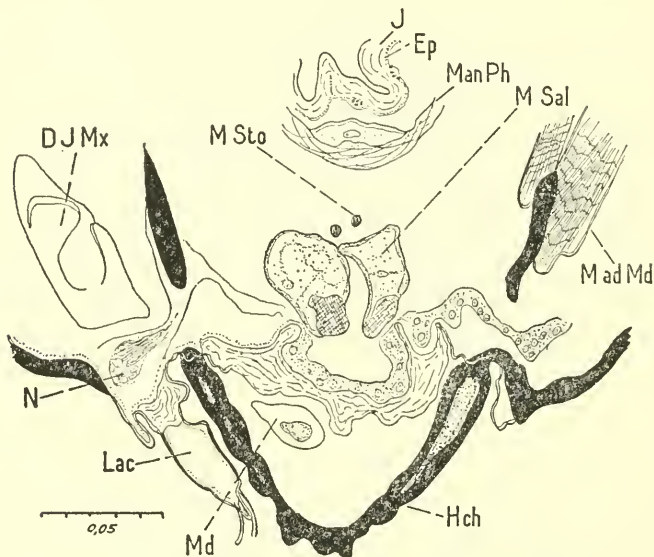


FIG. 2.—*Cricotopus* gr. *silvestris* Fabr.

Part of a cross section concerning the hypochilan region situated immediately before the insertion of the salivary muscle. Relationships of the hypochilum with the lateral cranial wall, the maxilla (*Lac*), and the mandible. Cf. fig. 4 of this paper and fig. 7 of Gouin (1957).

IMPORTANT MODIFICATIONS OF THE ORTHOCLADIAN STRUCTURE

THE DIAMESAN STRUCTURE

Among other characteristics Goetghebuer (1932, p. 145) mentions the presence of numerous hairlike setae implanted on the maxillary lobe and on the labium (hypopharynx auct.). In effect, the labial

⁴ The adaptative characteristics are rather to be found in the organs of progression, the prolegs. There is a very distinct difference in the manner of motion of standing-water species and of those haunting torrents. The former swim with spiral undulations of their bodies, while the latter move like caterpillars of the Geometridae, imitating very well the larvae of Tanyptinae.

processes, which in all the other forms, chironomid as well as orthocladian, are rather strong, rigid, and short, are in the genus *Diamesa* represented by tufts of long, tenuous setae, appearing to obstruct the atrium before the hypochilum. On its sides, the labium presents a row of short scales. Moreover, the lacinia is provided with setae instead of the knife-bladelike chaetae which the maxilla of *Cricotopus* bears; the ventral mandibular brush is made of tenuous setae. The whole gives the impression that the "mouth" is obstructed. On the other hand, the labral processes seem to be stronger; in effect, the sensillae I to IV have the form of minute points, and the chaetae and spinulae are represented by short spinulae situated in front of the ventral tormal arch ("margo labralis" of Zavřel). The hooklike form and the nondivision of the centroepipharyngeal chaetae are also points to be noted.

PRODIAMESA OLIVACEA MG., A PELOBIONTIC SPECIES

This detritivorous species of the *Diamesa* group, inhabiting mud of slow-flowing streams, presents some characteristics convergent with those of the *Chironomus* larva, especially in the labral and epipharyngeal processes. In effect, here, we find again the lateral and median labral chaetae ("chaetae" and "chaeta media" of Zavřel) finely pectinated, occupying the whole width of the ventral labral surface, a position very reminiscent of that of the *Chironomus* larva. In no lasiophagous species have these chaeta either this form or this disposition. The structures of the other organs have not such a clear convergence character. In the U-shaped piece, the hooks ("chaetulae laterales" of Zavřel) are rather long and very simple, but they do join; the premandible is strong, its distal tip is bifurcated and wide without a messorial brush. The labial processes are very different from that of the *Diamesa* larva: they include sensorial rods and setae, denticulate-edged scales and scales with minute points, disposed in several rows and strata; therefore the labium is not brushlike as in *Diamesa*. The hypochilum is characteristic of the species: its rather irregular outline, its wide basal winglike expansions with whiskers made of long setae, the deep pigmentation of the whole ventral region forming a design like an X, all give this larva an extremely characteristic aspect. Anatomically this region is not different from that of orthocladian larvae. The winglike setigerous expansions are only lateral processes of the hypochilan base as in *Cricotopus* and are thus not homologous with the striated plates of *Chironomus*.

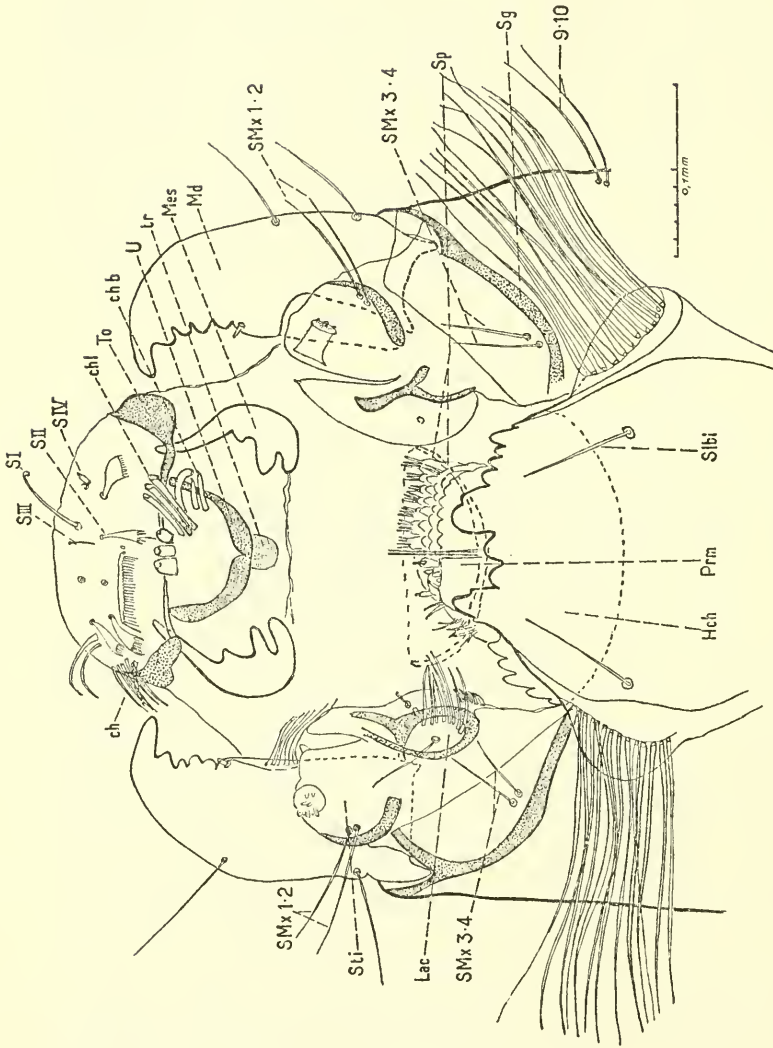


FIG. 3.—*Prodiamesa olivacea* Mg.

Ventral view of the buccal structures in their entirety. The even-numbered elements are figured only on one side; the superficial planes of the prementum are figured on the left side, the deeper planes on the right side, and the outline of the suspensorium is figured in stippling.

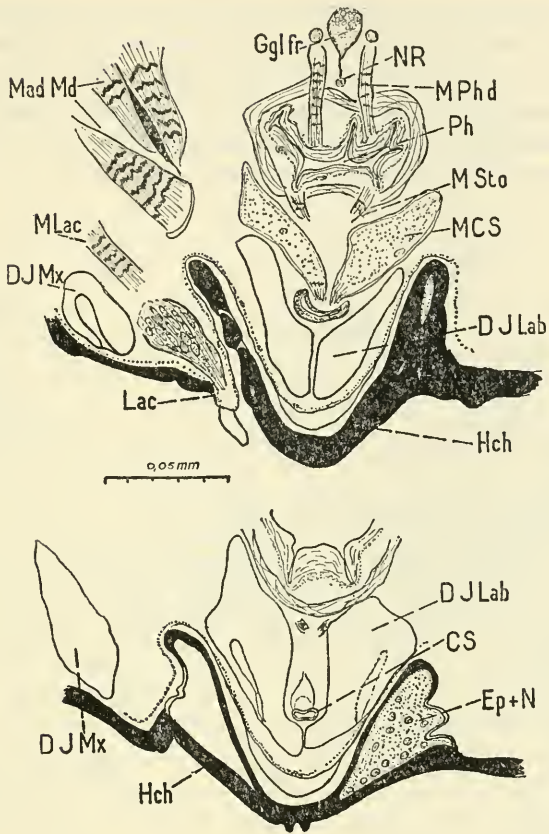


FIG. 4.—*Prodiamesa olivacca* Mg.

Inferior parts of two successive cross sections (10μ) concerning the hypochilan region. Conformation of the hypochilum with its base enlarged into a spacious cavity where there are numerous nerve elements. Location of the maxillary (*DJMx*) and labial (*DJLab*) imaginal discs. Cf. fig. 2 of this paper and fig. 7 of Gouin (1957).

THE PREDACEOUS MODIFICATION OF THE ORTHOCLADIAN STRUCTURE:
 PROTANYPUS MORIO ZETT.

Some species of Orthoclaadiinae and of the *Diamesa* group are predaceous or reputed to be so (cf. Thienemann, 1954, p. 57 sq.). Thus the *Cardiocladius* species are supposed to feed on the Simuliidae larvae among which they live. *Cardiocladius* sp. and *C. obscurus* Joh. (cf. Saunders, 1924) that we have examined present no special characters; but are not the Simuliidae larvae, the presumed victims of *Cardiocladius*, fixed upon a support? The *Pseudodiamesa* larvae

have an omnivorous regimen with carnivorous predominance; the larva of *Ps. behlingi* Fittkau (1954), which does not differ from *Ps. branickii* Now. and *Ps. nivosa* Goetgh., according to Fittkau (p. 93), shows nothing remarkable in its buccal structures. One could not, without invoking an interpretation, recognize in these structures a correlation with the alimentary regimen.

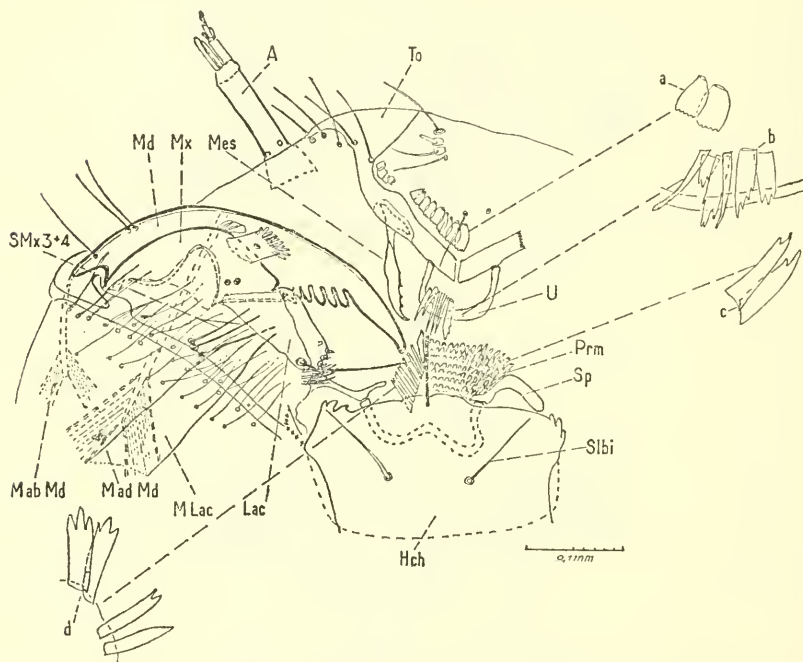


FIG. 5.—*Protanypus morio* Zett.

Partial view of the anterior ventral region of the head. *a*, two labral scales; *b*, some epipharyngeal elements; *c*, *d*, some premental elements. The prementum (before the hypochilum) shows its different typical processes, the left part being the more ventral. Cf. fig. 15 of Gouin (1957) and figs. 1 and 3 of this paper. After two preparations furnished by Prof. Hřábé (Brno) e coll. Zavřel. The cranium of these is broken along the line marked with plus marks (++++).

On the contrary they are much more distinct in the diamesan larva *Protanypus morio* Zett. (fig. 5), of which Zavřel (1926, p. 208 sq.) has already sketched the anatomy (cf. Goetghebuer 1932, p. 166). Being a form of lake benthose, it feeds on living prey, and in the intestine one finds remains of ingested Chironomidae larvae and pupae (cf. Thienemann, 1954, p. 57). The fundamental structure is indeed orthocladian, but presents an ensemble of remarkable modi-

fications. What strikes the student at first sight is the presence of numerous straight spine-shaped elements of variable dimensions, with one or two points; this character is particularly distinct on the epipharynx, the lacinia, and the labium (fig. 5 and figs. 1, 4). This prickly aspect is set off by the shape of the mandible with its long terminal tooth, and chiefly by the premandible. The latter in *Protanypus morio* is a straight club-shaped sclerite; its inner edge is furnished with a few short spines, and it ends in a rather stylelike and lightly curved point. The articulation is subproximal, the tendon being inserted on the internal extremity. This disposition of the application points gives great force to the muscle, which is an adductor. Lastly, it is a remarkable fact that the pharyngeal musculature, which is rather reduced in all the other forms, is in *Protanypus morio* very much enlarged and powerful and may contribute a great deal to the ingestion of the prey.

It is the general effect of these modifications affecting different organs which creates the individuality of the buccal structure, besides preserving the fundamental orthocladian dispositions of the labral and epipharyngeal ornamentations, and the mandibular, maxillary, and labial articulations. As the regimen of this species is well known, thanks to numerous analyses of intestinal content, and as it is known that it ingests its prey, one may deduce the correlations which the regimen, ingestion, and anatomical structure must have. In effect, the modifications of the orthocladian structural plan affect the epipharynx, premandibles, labium, mandibles, and in a way also, the hypochilum; to these is added the strength of the pharyngeal musculature. These modifications when taken all together form the distinctive features of the carnivorous orthocladian structure. The mandibular construction alone is not sufficient for deducing the regimen of the animal.

THE STRUCTURE OF PODONOMINAE

This group has been created and raised to the rank of subfamily by Edwards and Thienemann; Zavřel (1941) has analyzed the rather uniform labral structure of almost all known larvae. *Lasiodiamesa gracilis* K. (= *sphagnicola* K.) and *Trichotanypus posticalis* K. have been examined.

The structure, particularly the hypochilum, mandibles, and maxillae, is incontestably close to the orthocladian type. On the contrary, very distinct differences are found in the labral and epipharyngeal formations and clearly give an individuality to the Podonominae.

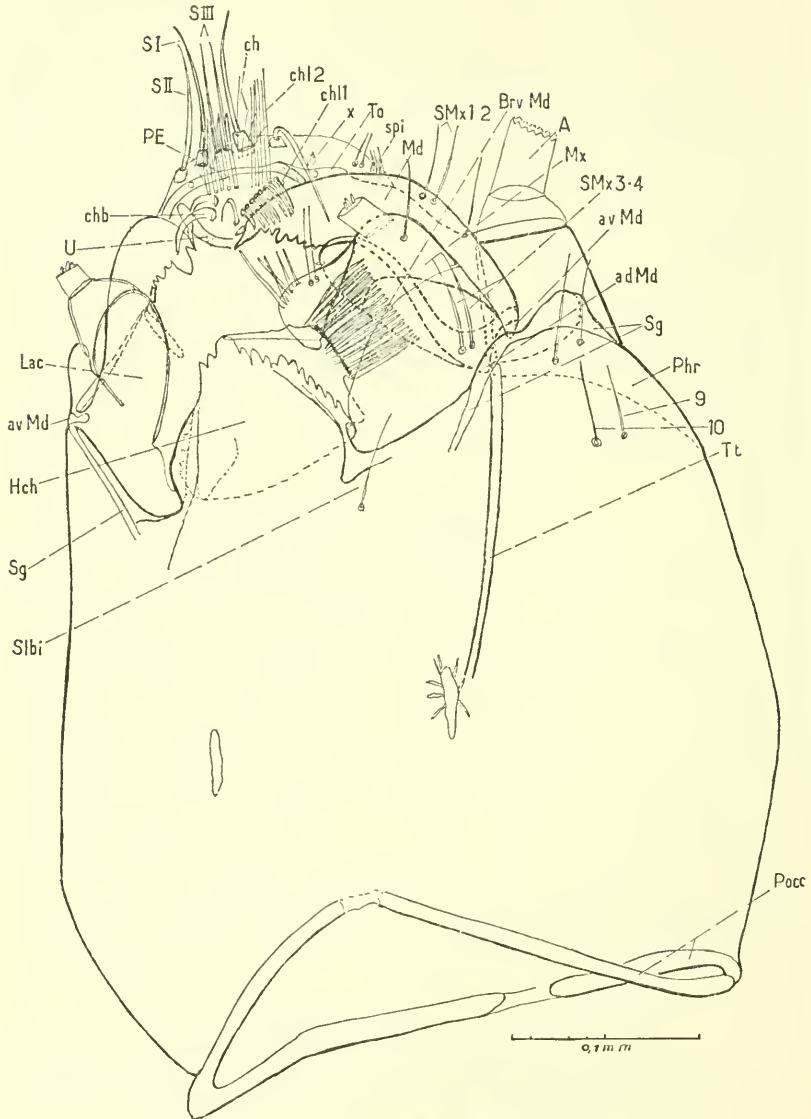


FIG. 6.—*Lasiodiamesa gracilis* K.

The ventral view, a little oblique, of the head shows (1) the netlike disposition of the labral and epipharyngeal elements designated according to Zavřel (1941); (2) the two groups of the centroepipharyngeal chaetae (*chl1*, *chl2*; (3) the little labral rod (*x*) beside the torma, and which Zavřel considers as the premandible; (4) the tentorium. The mandible, of which the ventral brush is disposed in a line, is concealed by the maxilla. The hypopharynx and the labium are not figured; they are situated in the space between the mandibles, the maxillae, and U-shaped piece, and the hypochilum. The even-numbered organs and elements (except *SI*, *SII*, *SIII*) are figured only on one side.

First of all, there is no premandible. Zavřel, it is true, identifies the premandible with a very short ventral appendage, more or less rodlike, inserted laterally on the labrum and somewhat proximal to the tormal arch. Very strictly speaking we might say that it is situated close to the usual mesorial insertion; but has it the connections, articulations, musculature, and innervation of this organ? The preparations in toto which Zavřel and I have examined do not allow us to answer this question, which can only be solved by studies of the living larva and histology. Whatever it is, this pretormal labral rod has neither the form nor the usual functions of the premandible. Therefore it is impossible to follow the Czech author on this point, for, in order to homologize two organs, they must have a minimum of structure to permit recognition of one connection at least (cf. Gouin, 1955).

The labral and epipharyngeal chaetae and setae have been very well described by Zavřel. They are remarkable in their numbers, dimensions, and disposition (fig. 6); the sensillae labri especially are very long and articulated on very high socles. The centroepipharyngeal chaetae are strong, curved hooks; the epipharyngeal comb is represented in *L. gracilis* by a few rather tenuous bristles, set in lines behind the tormal arch (this feature is rather variable in the different genera, cf. Zavřel); there are, besides, numerous tenuous chaetae disposed as in figure 6. This structure is characterized by a clear tendency to multiplication, lengthening, and tenuity of the labral and epipharyngeal hairlike processes; analogous features are also found on the lacinia. Finally, the multiplication of the mandibular and hypochilan teeth is a new example of the very clear correlations of these organs.

There is another important fact to be noted: the presence of a rudimentary tentorium. It has its origin on the internal phragma close to the dorsal mandibular articulation and proceeds obliquely nearly to the middle of the ventral wall where it ends, freely as it seems, near an oval superficial scar. The antennal socles are also supported by a parallelopipedic skeleton, and the whole preclypeal area is uniformly sclerotized. This tentorial arm recalls the Ceratopogonidae larval one (Gouin, 1955); the interantennal part might represent the dorsal tentorial arm.

FUNDAMENTAL CHARACTERISTICS OF THE CHIRONOMIAN, ORTHOCLADIAN, AND PODONOMIAN CEPHALIC STRUCTURES

After having studied the larval structures of *Chironomus* (Gouin, 1957), of the Orthocladiinae and Podonominae, and, before describing the anatomy of Tanyptinae, we will recapitulate these three

typical structures. They include the following dispositions and elements; their morphological interpretation is given by Gouin (1957).

a. The cranium is ventrally closed by a median sclerite (the "hypochilum"), double-walled, forwardly toothed, forming a rather convex vault. Its post-occipital margin is dorsally incomplete. There is a rudimentary tentorium. The frontal suture limits a triangular clypeofrontal area.

b. The very different labral and epipharyngeal ornamentations include: (1) the tormal sclerite which continues on the ventral face as a thin transversal bar; (2) the four pairs of sensory setae (sensillae labri I to IV); (3) the pair of premandibles articulated in a syndesis to the central tormal bar; (4) the diverse ventral chaetae (chaetae and spinulae of Zavřel) of which the median chaeta is often distinct from the others; (5) articulated to the tormal bar, the centro-epipharyngeal piece ("piece en U," "ungula" auct.); (6) in the centro-epipharyngeal area, the epipharyngeal comb, backed against the tormal bar, and chaetae ("chaetulae," Zavřel); (7) four pairs of muscles: the tormal muscle, two messorial muscles, the labro-epipharyngeal muscles.

c. The cibarial and pharyngeal musculature is reduced to a few fiber groups.

d. The mandible has obtuse molar teeth and an internal ventral brush; the condylic points of articulation are disposed on the "phragmata" and on an oblique axis, apposing the mandible to the hypochilan arch. There are two antagonistic muscles; the adductor, very powerful, is divided into four fiber groups.

e. The maxilla is regressive, its elements not very distinct, the sclerites reduced; its mobility is slight. There are a stipital muscle and a lacinial muscle which are rather feeble. The maxilla and mandible are closely connected.

f. The labium is membranous and regressive, hidden in great part by the hypochilum; a pair of premental muscles gives it a weak longitudinal mobility. Numerous sensorial elements are on its anterior end. The reduced hypopharynx is at the back of the labium from which it is separated by the salivary duct. The suspensorium constitutes the frame of the salivary syringe. The retractor angulorum oris (*rao*) is absent.

g. The muscular origins are grouped: (1) on the clypeofrontal triangular area; between the antennal socles (cibarial muscles); toward the middle (anterior messorial muscle); distally, toward the summit (posterior messorial muscle, pharyngeal muscles, tormal muscle); (2) in the dorsal lateral and ventral region of the posterior half of the cranium (mandibular muscles); (3) in the middle of the lateral ventral region (maxillary muscles); (4) between the posterior tentorial pits (labial muscles).

Differential characters of these three structural types:

a. The orthocladian structure is very close to the generalized organization plan. The labral and epipharyngeal processes tend to be spinelike or hook-shaped; the diamesan structure is an important modification of it, chiefly characterized by the setiform aspect of the labral and labial processes. Two diamesan forms are excepted: *Prodiamesa olivacea* Mg, detritivorus, with characters convergent with the chironomian structure; and *Protanypus morio* Zett., carnivorous.

b. The podonomian structure is distinct from the generalized organization plan and from the orthocladian structure by the construction, the dimensions,

and the assemblage of the labral elements, the absence of premandibles, the multiplication of the mandibular teeth and correlatively the hypochilan teeth.

c. The chironomian structure adds a few individual characteristics to the fundamental traits: (1) the labral and epipharyngeal elements are pectinate, particularly the very distinct individualized median chaeta and the centro-epipharyngeal chaetae; (2) correlatively the dorsal brush; (3) the presence of a brush close to the messorial tip; (4) the anterior part of the ventral wall is double, the internal wall (which is the "striated plate") is soldered to the hypochilan "rabat," correlatively with a different insertion of the maxillary base.

The general structure of the family is thus specified by these three modifications, typical for the subfamilies Orthoclaadiinae, Podonominae, and Chironominae. However, the great resemblance in the disposition, the connections, and the conformation of the constituent elements authorized the joining of these three types under the common term of "generalized orthocladian structure," for the orthocladian type is truly the structure which is nearest to the generalized type. To this structure is opposed the "tanypin" structure, very distinctly correlated with the strictly carnivorous regimen, the study of which forms the subject of the following section.

THE STRUCTURE OF TANYPINAE: THE LARVAL HEAD OF MACROPELOPIA CF. NEBULOSA MG.

The anatomy of the larval head of Chironomidae in the predaceous larvae of the species grouped in the subfamily Tanypinæ presents remarkable structural details. They have been the subject of a paper by Zavřel (*in* Thienemann and Zavřel, 1916-1917, p. 575 sq.), the data of which are reviewed and completed in the following study.

The whole behavior of these predaceous larvae, the length of the pseudopoda, the flexibility of the abdomen, the retractibility of the antennae, the falciform mandibles moving in frontal planes, the powerful cephalic cibarial and pharyngeal musculature, the extensibility of the oesophagus—all these characters and many others are strictly correlated with the mode of life. The animal, looking for its prey, advances in slow and rather extensive movements, often stops to explore the area by shaking its antennae, places its head and its thorax as if to proceed in a swift current, its abdomen, stretched like a spring, always highly buttressed above the posterior pseudopoda. Then, when it has thus been drawn by stages to within reach of its pseudopoda, with a sudden movement of relaxation it projects its body forward and implants its hooks into the soft body of its victim. It will ingest the prey completely, thanks to its maxillae being abun-

dantly provided with very supple bristles and also to the aspiration occasioned by the dilatation of the cephalic stomodeal cavities and the movements of the labiohypopharyngeal complex. It is not rare to find in the lumen of the strongly dilated oesophagus several Chironomidae larvae, and even to be able to identify them.

But apart from the mandible and maxilla described in detail by Zavřel (loc. cit., pp. 582-585, figs. 12, 13), the characteristics of which have just been recalled, the differences between the orthocladian (s.l.) and tanypin structures reside chiefly in the labroepipharynx and the stomodeum and in the complex labiohypochikan.

THE LABROEPIPHARYNX

The labroepipharynx has only a few sensory setae, which are either rods or vesicles with an innervated chaeta (cf. Zavřel, loc. cit., pp. 579-582, figs. 7 to 11). No hooks, combs, other sclerites, or premandibles are present; we find no trace in *Macropelopia* of all the very abundantly differentiated labroepipharyngeal details of the orthocladian larvae. Only the labroepipharyngeal constrictor and tormal muscles exist; the latter has two-fiber groups, one having its origin almost in the middle of the frontoclypeus, the other, stronger and more lateral, being attached to the back of the head. The "premandibular vesicles" ("Praemandibularbläschen") of Zavřel are only labroepipharyngeal expansions without muscular connections. The clypeofrons is enlarged posteriorly.

The cibarial atrium and the pharynx in its cephalic parts are endowed with a powerful musculature, the radiated dilators of which present a very characteristic X-shaped design on the cranium (cf. Zavřel, loc. cit., figs. 3, 4).

The whole of this musculature comprises the six following groups (figs. 9 to 11): (1) the dilatores cibarii (*MCib*) with numerous fiber groups, anterior to the frontal ganglion, here particularly developed; the homologue in the orthocladian forms has only three or four very slender fiber groups; (2) the anterior dorsolateral dilatores pharyngis (*Ph dla*); (3) the posterior lateral dilatores pharyngis (*Ph dlb*); (4) the ventral dilatores pharyngis, posterior and lateral (*Ph vl*); (5) the median dilatores pharyngis, posterior and dorsal, with finer fiber groups the origins of which are disposed along the sagittal line (*Ph dm*); (6) the pharyngeal circular muscles, antagonistic to the dilatores, against which the very slender internal stomodeal longitudinal fibers lean (*M ann*).

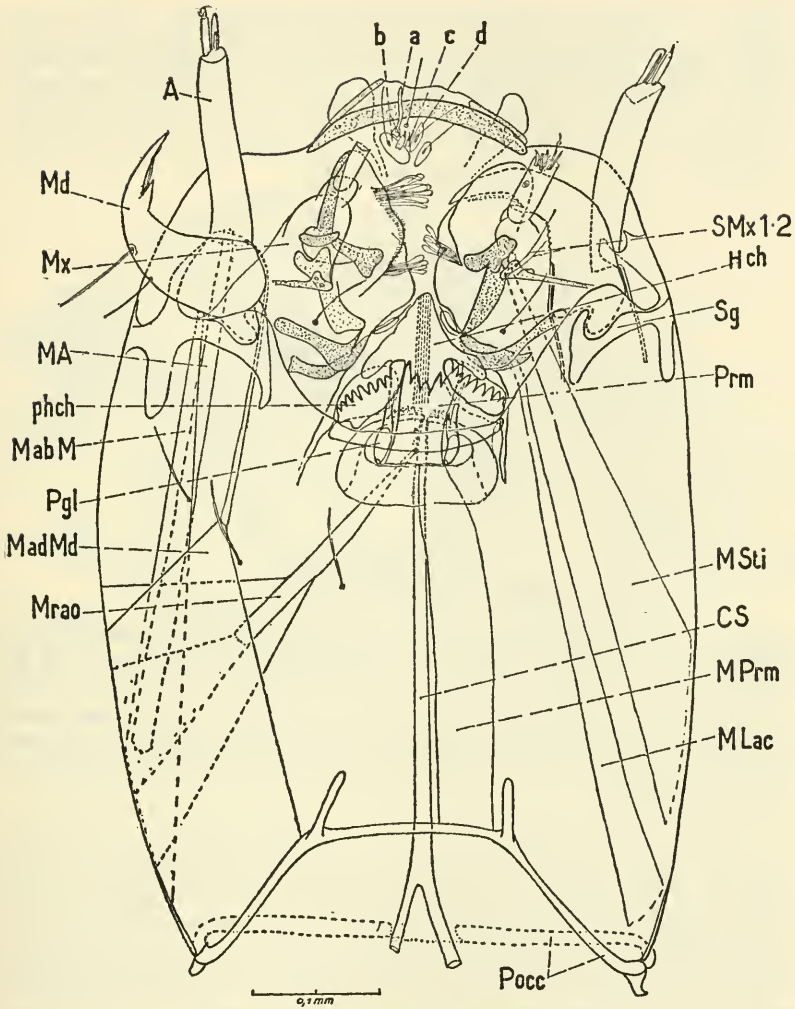


FIG. 7.—*Macropelopia* cf. *nebulosa* Mg.

Ventral view of the head showing the entire structure. *phch*, hypochilan comb.

THE VENTRAL REGION

The structures of the posterior cephalic part have been well described by Zavřel. Let us remember that the median and anterior cranial wall is made up of a vaguely triangular membranous area (so-called "labium" of authors), homologous with the strongly sclerotized and toothed hypochilum of *Chironomus*. The *Macropelopia* hypochilum is basically flanked by two superficial "paralabial"

combs; its axis is occupied by the "pseudoradula," a rugose band, which is a thickening of the inner surface; in sections, the hypochilum appears as a fold enclosing a rather wide cavity communicating at the back with that of the head. It is not opposed to the mandibles as is that of the other Chironomidae. There are no maxillary plates.

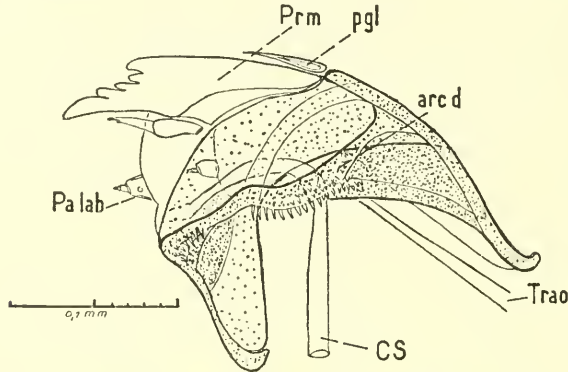


FIG. 8.—*Macropelopia* cf. *nebulosa* Mg.

Dorsal three-quarter view of the labial and hypopharyngeal skeleton, slightly reversed in the stomodeal lumen (which in the figure would take place on the left side). *Prm*, prementum ("epilabium" or "glossa" auct.); *pgl*, "paraglossal" scale flanking the prementum; *arc d*, dorsal arch of the hypopharyngeal skeleton bearing the double fringe of teeth; *Trao*, tendon of the retractor angulorum oris, which is inserted near the toothed fringe; *CS*, the single salivary duct; *Pa lab*, labial palp.

A little to the back appears the labiohypopharyngeal complex (s.str.), supported by a rather complicated skeleton (fig. 8). In sagittal sections it appears as a fold of the basal buccal atrium; in *Macropelopia* it gives the distinct impression of a unit, for the salivary conduit (the fusion of the two tubes is formed on their entrance in the head) does not widen in the large meatus which in *Chironomus* deeply separates the hypopharynx from the labium.

Externally, the labium of this complex has a kind of strongly sclerotized shield, toothed on its anterior extremity (so-called "glossa" or "epilabium" of authors) and bound by a membrane to the hypochilan tegumentary fold. At its base the labial or premental muscle is inserted (fig. 13). The homologue of this shield in *Chironomus* is only lightly indicated by a slight sclerotization. Moreover, dorsally to this premental shield, but a little to the back, the labium is furnished with papillae, and more especially, with two lateral palpiform innervated organs.

What Zavřel calls "Hypopharyngealgerüst" is principally a sclerotized ring surrounding the complex and supported by the prementum (fig. 8); the dorsal (hypopharyngeal) arch is fringed with steellike teeth.

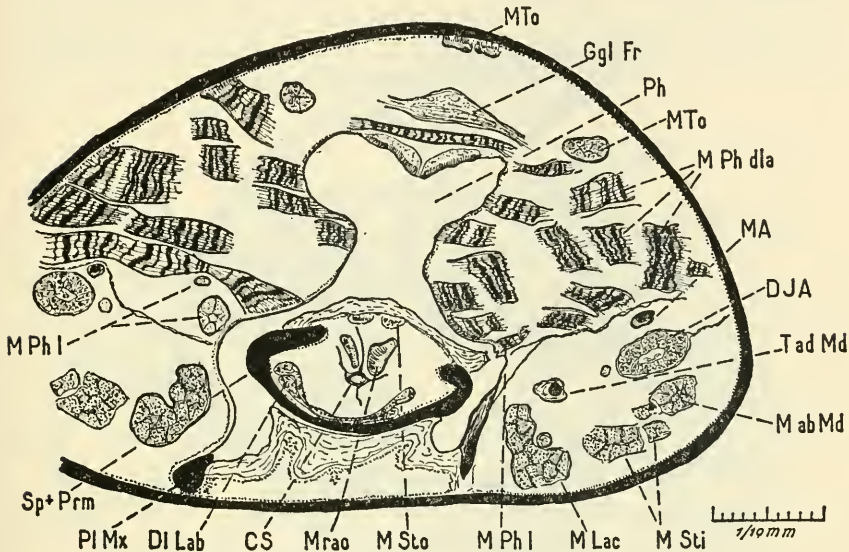


FIG. 9.—*Macroploopia* cf. *nebulosa* Mg.

Part of a cross section situated on the level of the frontal ganglion, the origins of the internal tormal fiber groups (*MTo*) and distally from the glossal teeth. A double membrane separates the antennal muscle and imaginal disc from the set of the pharyngeal muscles; the cavity included by that double membrane widens toward the front into a broad cleft communicating with the pharynx and embracing the antennae. The external tormal muscle origins are situated a few sections farther back laterally on the cranium; the two fiber groups are inserted forward on the membrane itself, constituting the roof of the preoral cavity; there is here no sclerotized differentiation. The blood, very abundant, is not figured.

The musculature of these organs comprises only two muscles, of which one is not found in the generalized orthocladian structure (figs. 9, 10); they are: (1) the true labial or premental muscle (*M Prm*), the *mI* of figure 18 of Zavřel; (2) the retractor angulorum oris (*Mrao*), opposite to the premental muscle, directed dorsally, posteriorly, and diagonally. Zavřel designates it by *m3* (fig. 18) and *mh* (fig. 47). Its tendon is inserted on the basis of the toothed fringe of the dorsal hypopharyngeal arch; this muscle, which bifurcates into two powerful fiber groups surrounding the antennal muscle, takes its origin on the posterior part of the cranium.

We have not found a trace of a salivary muscle either in cross or longitudinal sections, nor on the preparations in toto. It therefore seems that the swaying movements of the labiohypopharyngeal complex contribute toward evacuating the product of the secretion

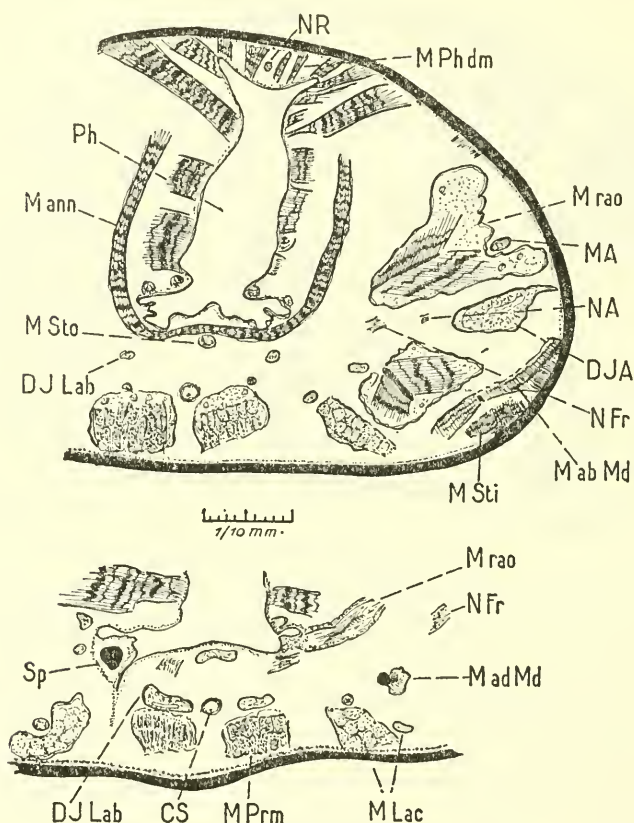


FIG. 10.—*Macropelopia* cf. *nebulosa* Mg.

Parts of the two cross sections passing almost to the posterior quarter. The upper figure shows the connections of the *rao* blending together the slender antennal muscle between its two divergent fiber groups. The lower figure passes farther forward and shows the level of insertion of *rao* on the suspensorium.

of the prothoracic labial glands; it is true that the Tanypinae larvae do not construct silken cases.

The mobility of this whole structure is then rather great, much greater than that of the homologous organ in the orthocladian larvae. In effect, the retractors angulorum oris (*Mrao*) reverse the complex in the stomodeal lumen, the premental and hypopharyngeal teeth by

these swaying movements carry away the ingested prey and lacerate its integuments. The return of the organ to its rest position is assured by the premental muscle, acting on the premental basis. This same muscle, quite strong in *Macropelopia* but very slender in *Chironomus*, gives the labium a backward movement, the opposite movement being effected by the elastic membranes alone or combined with the action of the retractor angulorum oris.

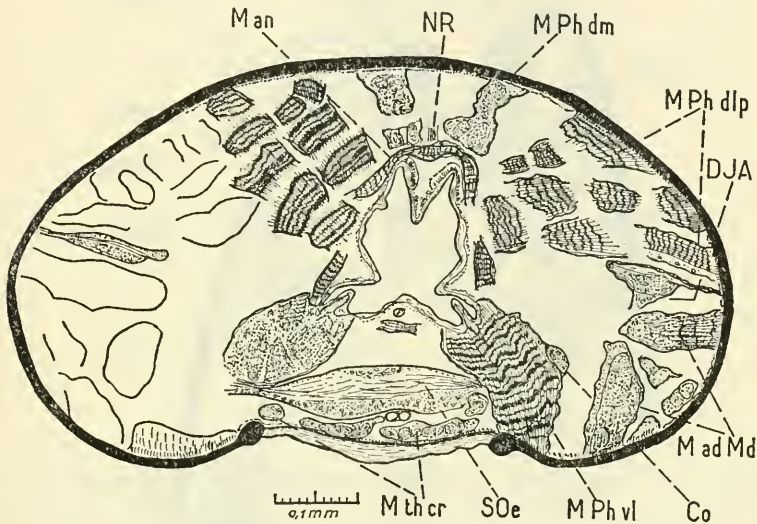


FIG. 11.—*Macropelopia* cf. *nebulosa* Mg.

Part of a cross section passing through the pharyngeal ventral and lateral dilators (*M Ph vl*), which are situated behind the circumoesophageal connective and might correspond to No. 44 of Snodgrass (1929). The section meets the salivary ducts immediately behind their point of union.

THE LARVAL FORMAL TYPES IN CHIRONOMIDAE

The organization of the predaceous Tanypinæ larvae, the close correlation of which with behavior we have just mentioned (p. 187), differs from that of the orthocladian (s.l.) larvae by a set of characteristics of which the "dominant" ones are: (1) the extreme development of the cibarial and pharyngeal cavities and, correlatively, of the radial and circular muscles just as in the case of the clypeofrons; (2) the labroepipharyngeal armature is extremely reduced; (3) the form of the mandibles and their movements in a horizontal plane; (4) the particular structure of the labiohypopharyngeal complex which assumes the transport of the ingested food, while in the

other types this role is taken over by the mandibles in great part; (5) the weak sclerotization of the hypochilum, permitting some dilatation of the cephalic cavities, while its homologue in the other types, strongly sclerotized, is opposite to the mandibles.

The Chironomidae larvae present in their feeding organs four structural types (Gouin, 1956): the orthocladian, podonomian,

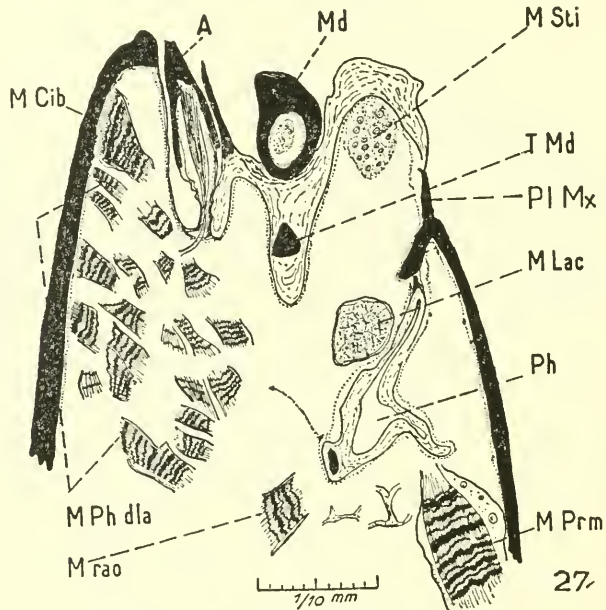


FIG. 12.—*Macroploopia* cf. *nebulosa* Mg.

Part of a lateral sagittal section. It shows the relationships of antenna partly invaginated and innervated (*A*) with the mandible (*Md*) and maxilla (*Mx*), of which the section, passing to the outside of the palpus, grazes the stipital muscle (*M Sti*) very close to its insertion; the maxillary plate (*Pl Mx*), a kind of fold of the cranial wall, supports the basal maxillary sclerite. In the thickness of the integumental membrane, the mandibular adductor tendon (*TMd*). Near the premental muscle, some nerve elements.

chironomian, and the tanypin types. The anatomy of the digestive tract (Gouin, 1946) shows a very clear parallelism: the Tanypininae, in effect, form again a type well defined by the great voluminous mesenteric cells with papillae situated behind the cardiac valve (Gouin, 1946a, fig. VII). On their part, the Chironominae present a "style" of their own and particularly the very richly differentiated structure of the cardiac valve, mesenteron, and proctodaeum, so clearly different from the anatomically simple intestine of the orthocladian and pod-

nomian larvae (Gouin, 1946a, 1946b), these two types being in this particular rather similar. The larval tracheal system is more reduced in Chironominae larvae than in the others.

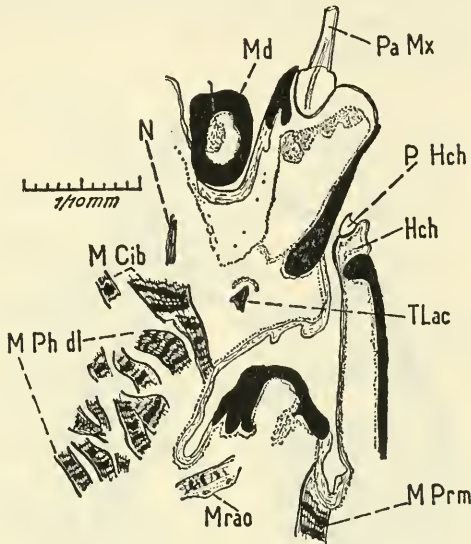


FIG. 13.—*Macropelopia* cf. *nebulosa* Mg.

Part of a sagittal section passing on the level of hypochilan combs (*P Hch*). It shows the connections of the hypochilum (*Hch*) and the combs with the cranial wall, the insertion of the premental muscle (*M Prm*), some fiber groups of the pharyngeal dilators (*M Ph dl*), and the muscle *Mrao*. The mandible shows an innervated seta; the maxilla shows an innervated part of palpus (*Pa Mx*) and the ventral basal sclerite (cardo p.p.); the tendon of the lacinial muscle (*TLac*) is tangentially cut.

SOME REMARKABLE RELATIONSHIPS IN THE GNATHAL REGION

After this detailed study of the structural types of Orthoclaadiinae, Podonominae, and Tanypininae and that of Chironomidae (Gouin, 1957), I shall attempt to deduce some outlines of the relationships between the organs of the gnathal region. Though the data of authors are unfortunately rather rare, two aspects can be evoked.

RELATIONSHIPS BETWEEN THE MANDIBLE AND THE HYPOCHILUM

In the lower Nematocera larvae (*Trichocera*, *Mycetobia*, *Rhyphus*), Anthon (1943) describes a conformation of the mandible; he considers it as being divided into two segments, of which the distal one

moves on the basal one. Reviewing Anthon's paper, Snodgrass (1950, pp. 75-76) rightly claims that "it is impossible to accept Anthon's conclusion," just as I have already rejected Anthon's interpretation concerning the larval Chironomidae mandible (Gouin, 1957). According to Snodgrass, it is merely a partial "desclerotization," permitting a weak mobility.

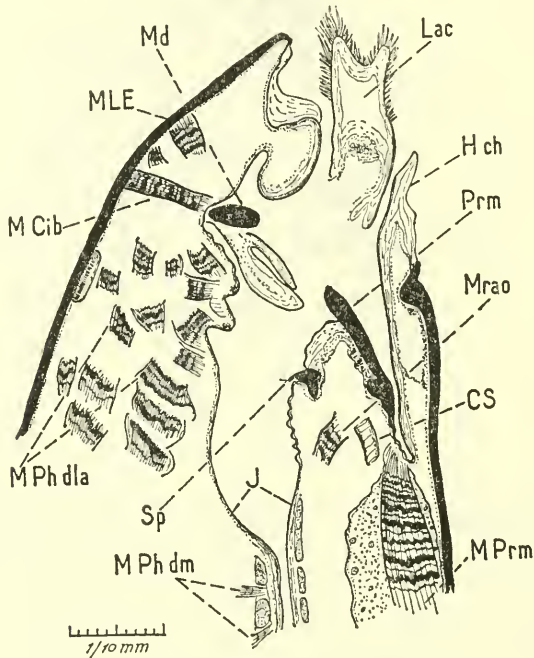


FIG. 14.—*Macropelopia* cf. *nebulosa* Mg.

Part of a paramedian sagittal section more lateral than that of figure 15. Insertion of the premental muscle (*M Prm*); section of the maxillary lobe (*Lac*) with the insertion of numerous club-shaped bristles. The mandible (*Md*) is cut on the extreme tip. The suspensorium (*Sp*) shows an element of its toothed fringe. Stomodaeal circular musculature; pharyngeal lateral and dorsal dilators. *J*, intima.

Whatever it is, such a segmentationlike conformation exists on the mandibles of these larvae; and Schremmer (1951) has also described it in some Brachycera. Besides, the mandible being prehensile, as has been stated (Gouin) in *Chironomus* and also in forms studied by Anthon (figs. 31, 33), the adductor tendon is inserted on the base of the toothed part.

It is therefore interesting to look for the correlations of the mandible with the other structural elements, especially the hypochilum. Alluding to the disposition of the points of the articulations, Schremmer claims that when the mandibles move in a horizontal plane, they are not "segmented." This is precisely the case in Tanypinæ larvae:

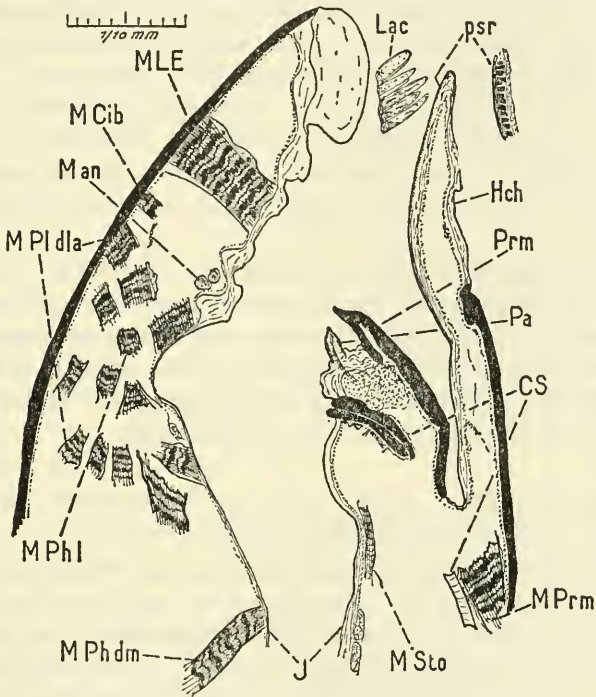


FIG. 15.—*Macropelopia* cf. *nebulosa* Mg.

Part of a nearly median sagittal section. It shows the relationships of the structural elements of the ventral cephalic region, innervation of a labial palpus; premental sclerite and its hinge of articulation; the salivary pump and the insertion of its muscle on its ventral sclerite. The labroepipharyngeal muscles (*MLE*); the club-shaped maxillary bristles (*Lac*) are grazed. Detail of the "pseudoradula" (*psr*) on the right.

their mandibles are opposed to each other and the hypochilum, normally constituted, is membranous.

But in other Nematocera, the mandibles move in intermediate planes between the frontal and sagittal ones. It is then established that the unsegmented mandible exists in the types of which the hypochilum is well formed, sclerotized, and is the fixed jaw of pincers

(e.g., *Chironomus*, *Cricotopus*, *Lasiodiamesa*, and numerous others). On the contrary, the species with a "bisegmented" mandible have no hypochilum; and there is a very clear progression in these primitive forms, which Anthon describes. Thus the hypochilum is absent and the mandible is "segmented" in *Trichocera*, *Mycetobia*, and *Rhyphus*, while *Ptychoptera* shows only an immovable mandibular lobe corresponding to the incisor part, and its hypochilum is only imperfectly formed. The third example of this progression, *Philosepedon*, has the mandible unsegmented and the hypochilum developed.

The writer's indications are too summary to warrant a precise statement about these correlations. But the relationships between the mandibular functions, the axis of rotation, and the absence or presence and structure of the hypochilum are too striking not to be emphasized.

These relationships might be summed up thus: The mandible is only "bisegmented" in the forms where it moves in an oblique plane and in which the hypochilum is absent. It is unsegmented when it is opposed to a sclerotized hypochilum or also when it moves in a horizontal plane, the two mandibles being opposite to each other; in this case, the hypochilum is often membranous.

THE RELATIONSHIPS OF THE MAXILLA, THE LABIUM, AND THE HYPOPHARYNX WITH THE HYPOCHILUM

Between the maxilla and the hypochilum this "balancing" of the organs is again to be noted. Generally in the Nematocera, the maxilla is strongly reduced as compared with the orthopteran structure, and includes only the following elements, which are not always differentiated: The cardo with two bristles; the palpigerous stipes identified by the muscular insertions, besides being endowed with two setal and other cuticular processes; the lacinial lobe furnished with an extremely variable and differentiated armature; a very reduced skeleton. But the Mycetophilidae (Madwar) present a striking structure of the maxilla which in some types takes a mandibular form and functions.

The cellular and noncellular processes on the maxilla of the primitive groups such as *Trichocera*, *Mycetobia*, and *Rhyphus* (Anthon) are extremely abundant and various, evident signs of important functions. In these forms, as we have already pointed out, the hypochilum is absent, and the genus *Philosepedon* here again presents an intermediate character, which has already been seen in the structure of the mandible. In the Mycetophilidae (Madwar, 1937), the develop-

ment of this appendage is likewise related to the reduced hypochilum. In the Tanyptinae (p. 189) of which the hypochilum is membranous and relatively narrow, the maxillae are very much developed; and there would be numerous other examples.

As to the labiohypopharyngeal complex, it shows relationships with the hypochilum that may be compared with those of the maxilla; therefore, we find again a parallel progression. In the forms nearer to the fundamental structure studied by Anthon, the labium and hypopharynx (passing the labium forward) are well constituted and abundantly furnished with setae, chaetae, and other various cuticular processes; they then have complex and important functions.

Moreover, the formation of a sclerotized hypochilum goes with the structural and functional reduction of the labium and hypopharynx. *Philosepedon* (Anthon) shows again an intermediate point of this progression, in which reduction reaches its highest degree in the other Nematocera: Culicidae (Schremmer), Simuliidae (Grenier); Ceratopogonidae (Lawson; Gouin, 1955a), Chironomidae, and others. In the last named, the Tanyptinae (cf. supra, p. 189) in a way furnish the proof a contrario: the hypochilum is rather reduced and membranous, the labiohypopharyngeal complex is more developed than in the other Chironomidae.

There are therefore assured and precise relationships between the hypochilum on one side and the maxilla and the labiohypopharyngeal complex on the other; the development of the former is in a way contrary to the latter.

It has been possible only to sketch the correlations between the gnathal appendages and the conformation of the anterior ventral cranial wall. In fact, only an exhaustive morphological study will let us draw our conclusions with certainty. It is clear, after the preceding report, that for such a study the morphology, as Snodgrass claims, "must be intimate with function."

ABBREVIATIONS USED ON THE FIGURES

<i>A</i> , antenna; antennal.	<i>Co</i> , connective.
<i>ad Md</i> , dorsal mandibular articulation.	<i>CS</i> , salivary duct or pump.
<i>arc d</i> , dorsal arch of the hypopharyngeal skeleton.	<i>DJA</i> , antennal imaginal disc.
<i>av Md</i> , ventral mandibular articulation.	<i>DJLab</i> , labial imaginal disc.
<i>ch</i> , labral "chaeta" (Zavřel).	<i>DJMx</i> , maxillary imaginal disc.
<i>ch b</i> , posterior centroepipharyngeal chaeta ("chaetula basalis," Zavřel).	<i>Ep</i> , epithelium.
<i>ch l</i> , lateral centroepipharyngeal chaeta ("chaetula lateralis," Zavřel).	<i>Ggl fr</i> , frontal ganglion.
	<i>Hch</i> , hypochilum.
	<i>HPH</i> , hypopharynx.
	<i>J</i> , intima.

<i>Lab</i> , labium.	<i>P E</i> , epipharyngeal comb.
<i>Lac</i> , lacinia.	<i>Ph</i> , pharynx or pharyngeal.
<i>M</i> , muscle(s).	<i>phch</i> , hypochilan comb.
<i>Ma</i> , antennal muscle.	<i>Phr</i> , phragma.
<i>M ab Md</i> , mandibular abductor muscle.	<i>Pl Mx</i> , maxillary plate.
<i>M ad Md</i> , mandibular adductor muscle.	<i>Prm</i> , prementum.
<i>M an</i> , annular muscle(s).	<i>psr</i> , "pseudoradula."
<i>M Cib</i> , dilatores cibarii.	<i>S I-S IV</i> , labral sensory setae ("Sensillae labri," Zavřel).
<i>M C S</i> , muscle of salivary pump.	<i>Sg</i> , subgena.
<i>Md</i> , mandible.	<i>Slbi</i> , labial seta.
<i>Mes</i> , premandible or mesorial.	<i>SMx</i> , maxillary setae.
<i>M Lac</i> , lacinial muscle.	<i>SOe</i> , suboesophageal ganglion.
<i>MLE</i> , labroepipharyngeal muscles.	<i>Sρ</i> , suspensorium.
<i>M Ph vl</i> , pharyngeal ventral and lateral dilators.	<i>spi</i> , labral "spinula" (Zavřel).
<i>M Prm</i> , premental muscle.	<i>Sti</i> , stipes.
<i>Mrao</i> , retractor angulorum oris.	<i>T ad Md</i> , tendon of mandibular adductor muscle.
<i>M Sti</i> , stipital muscle.	<i>To</i> , torma.
<i>M Sto</i> , stomodeal muscle.	<i>tr</i> , centroepipharyngeal trapezoidal piece.
<i>M Th cr</i> , thoracocranial muscle.	<i>Trao</i> , tendon of the retractor angulorum oris.
<i>MTo</i> , tormal muscle.	<i>Tt</i> , tentorium.
<i>Mx</i> , maxilla.	<i>U</i> , centroepipharyngeal U-shaped piece.
<i>NA</i> , antennal nerve.	
<i>N Fr</i> , frontal ganglion connective.	
<i>N R</i> , recurrent nerve.	
<i>Pa</i> , palpus.	

The arabic figures designate the cephalic sensory setae.

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THE PROBLEMS OF "MORPHOLOGICAL ADAPTATION" IN INSECTS

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(WITH 20 PLATES)

In 1955 I published in *Atti dell'Accademia Nazionale dei Lincei* a paper, illustrated with 25 plates, on the problems related to the "morphological adaptation" of the insects that have a specialized diet.¹ In the same year I presented a summary (without illustrations) of this paper for the volume of the Centennial Anniversary of the *Société Royale d'Entomologie de Belgique*.² Both of these contributions were published in Italian.

Now, as I have been invited by the Smithsonian Institution to contribute to the volume to be printed in honor of Dr. R. E. Snodgrass, I have thought that it would be advisable to let American biologists know directly and concisely (namely, with a short summary brought up to date with the latest findings) what I have discovered during my researches on the morphology, ethology, and ecology of the insects with a specialized diet, and also the deductions derived from the achieved results.³

Whoever has had the opportunity to consult the works dealing with the complex problems of the so-called "morphological adaptation" must have observed that the authors' references generally concern a rather limited number of taxonomic groups of living things. As a result the animal kingdom has been studied only partially, and the immense world of insects has been almost neglected. Yet it is a world which has displayed and more and more will display in the future a notable assemblage of structures and behaviors, the knowledge of which will perhaps be of the greatest importance for the solu-

¹ Grandi, G., *Gli Insetti a regime specializzato ed i loro adattamenti morfologici*. *Atti Accad. Naz. Lincei. An. CCCLII, Mem. Class. Sci. Fis. Mat. Nat.*, ser. 8, vol. 5, sez. 3, fasc. 1, pp. 1-60, 25 pls., 1955.

² Grandi, G., *Gli Insetti ed i problemi dell'adattamento morfologico*. *Mém. Soc. Roy. Ent. Belgique*, vol. 27, pp. 252-275, 1955.

³ In order not to burden the present note with the long list (70) of the bibliographical references of my publications on the subject, I refer to my paper in *Atti dell'Accademia Nazionale dei Lincei*, where the above-mentioned papers are almost all recorded.

tion of some of the fundamental problems of adaptation and transformism. For this reason I have for years been led to investigate such a rich field and consequently have discovered a series of facts which I think will be useful in the elucidation of the controversial subject.

I have studied larvae and adults of several species of holometabolic and hypermetabolic insects belonging to various families of the Lepidoptera, Coleoptera, and Hymenoptera. I shall arrange my observations in groups according to the taxonomic order, dealing first with preimaginal stages. Facts, suitably coordinated, will support my affirmations, and useless discussions will be eliminated. Finally, the general conclusions reached by me will be presented, summed up in 18 distinct units.

I. LARVAE OF LEPIDOPTERA (ERIOCRANIIDAE, NEPTICULIDAE, TISCHERIIDAE, GRACILARIIDAE)

The larvae of Lepidoptera which pass a part or the whole of their postembryonic development within leaves (as miners) are very numerous. There are some which develop and pupate within their mines, some which develop within the mines but pupate outside, and others which begin their development endophytically and end it ectophytically. A larva, when it is forced to move in the body of a vegetal tissue, goes about overcoming the resistance of the medium or utilizing it. To overcome it, the most expeditious way is that of eating the tissue. For making use of this resistance, if the mine is low and narrow, it is most suitable to set the head capsule at prognathism, reduce thoracic and abdominal limbs to simple protuberances or replace them with "ambulacral areolae," make somites jutting sidewise, etc. Well, we shall see how most of the changes undergone by the larvae of leaf-mining Lepidoptera are actually related to the various methods of taking food and ways of boring mines.

Indeed if we take into account some *Homoneura* and *Heteroneura* *Monothrysis* such as *Allochapmania* Strand, *Nepticula* Zell., and *Tischeria* Zell., which bore intraepidermic or subepidermic mines in the leaves, pupating in the same place (inside or outside the mine) or in the ground, we see that their larvae perform their whole development in the leaves of the host plant, but do not change their form radically during the development (a true and simple holometabolism or euholometabolism). They exhibit a more or less flattened body, prognathous head capsule caudad continued by two large dorsal plates invaginating within the thorax and strengthened by rather

conspicuous tegumental apodemata (the dorsal, longitudinal, and submedian apodemata may converge again posteriorly or are subparallel); the palate tends to differentiate anteriorly more or less conspicuous hairlike processes; the gnathites are little modified; the segments of the body are more or less considerably protruding on the sides; the thoracic and abdominal legs are generally involuted, subatrophied, or have disappeared and are often replaced with ambulacral areolae (the thoracic legs are the first to disappear), and so on. These modifications (partly resulting from the involution, rudimentation, and atrophy of organs, partly from the deformation of preexistent organs or from the development of new organs) do not seem to be always correlated and are considered to represent a complex of not very important "adaptations" by which a larva is able to live, move, and feed within vegetal tissues of a particular type without (it might be said) the hindrances of a cumbersome body structure. Instead, if we give attention to other Lepidoptera Heteroneura, Dithrysia and miners, too, such as the Phyllocnistidae belonging to the genus *Phyllocnistis* Zell., and Gracilariidae belonging to the genera *Gracilaria* Zell., *Acrocercops* Wallengr., *Oecophyllembius* Silv., *Lithocolletis* Zell., etc., we are in the presence of hypermetamorphic insects having a first larval phase with a generally plasmophagous diet, and morphologically very much modified, and a second type which may be eruciform, histophagous, endophytic or ectophytic, or a "sui generis" astomous, aphagous form which has the sole function of constructing the cocoon for the metamorphoses. It is necessary briefly to examine these larvae.

In the ultraspecialized larvae of the first phase the body is flattened; the head capsule is prognathous, very greatly flattened, sclerotized at the side edges, crossed by strong apodemata, of which the submedian longitudinal ones diverge backward, posteriorly and dorsally continued with two large laminae, which are invaginated within the thorax; ocelli are very much reduced in number and size; the mouth parts are deeply transformed (the labium and prelabium have been transformed into two wide, transverse, superposed laminar organs, between which the very flattened mandibles move in the horizontal plane; the maxillolabial complex without lobes, palpi, and sericarpous papilla is blended and sclerotized and, having become an integral part of the head capsule, in correlation with prognathism, closes it underneath like a throat); the tentorium is displaced backward; the body segments projecting laterally are separated by deep constrictions (the 10th urite is more or less exceptionally lengthened

and bifurcated), with the integument tending to differentiate papilliform or hairlike processes and reduce conversely the length of the hairs of its normal thricotaxis; the thoracic and abdominal legs are absent or sometimes partly replaced by "ambulacral areolae," which cannot be explained in any way as neof ormations or residues of legs. These larvae, as we have said, are plasmophagous and bore rather low and subepidermal or epidermal mines.

Near these, however, we find others in which the process of transformation appears less advanced and shows us the way that has been followed in arriving at the extreme conditions.

It is unnecessary to dwell upon the cruciform larvae of the second phase, but the others are worth particular attention; they are peculiar subcylindrical larvae, normally consisting of the head and the usual segments, which, however, do not project on the sides; moreover, they are astomous, aphagous, anophthalmous, and apodous with a highly reduced thricotaxis; in the broad, shortened head capsule without hind processes and with apodemes nearly obliterated, the antennae look like small membranous cups; the labrum is atrophic and coalesced with the clypeal region; the mandibles are subatrophied and united with the cranial wall; the maxillae also are intimately united with the postlabium, but furnished with palpi; the labium is furnished with palpi and spinneret; the mouth opening is absent. If these larvae had not a well-defined function, that of constructing the cocoon, we should be tempted to consider them as quiescent forms with involute anatomy.

The passage from the first to the second larval phase, as it has been pointed out in *Lithocolletis* Stgr., occurs through a mechanism that externally does not differ at all from the process of moulting of the former and later instars.

What can we deduce from the modifications of structure very briefly outlined above? Even now it is necessary to acknowledge that in a broad sense an endophytic (more exactly endophyllous) life does not require that the larvae, which have to live it, undergo any modification, when a strictly plasmophagous diet has not been considered as a necessity (and it is not understood why it should be so considered). But if we admit such necessity or consider the fact in itself that there are actually larvae mining leaves in the above-mentioned way, we must acknowledge that: (1) the above-mentioned larvae have reduced or eliminated all that was unnecessary or cumbersome to their movements and dietetical activity in the special microhabitat where they abide; (2) they have displaced the organs

which required under the same conditions a different position; (3) they have modified those which required modifications to function in a particular way; (4) they have acquired new structures suitable for helping the others in the work; (5) finally at a given time of their postembryonic development, by changing place, activity, or ways of feeding they are able to rebuild some of the organs previously lost, and conversely to lose others which before were present and functioning, or to be completely transformed by taking again through a simple moult the classic habit of eruciform larvae, which they had left, suitable, i.e., for accomplishing a kind of reversion of their ontogenetical evolution even though adaptative.

II. LARVAE OF PHYTOPHAGA COLEOPTERA (BUPRESTIDAE, CHRYSOMELIDAE, CURCULIONIDAE)

In this section I shall take into account, among the larvae of Coleoptera, some that have a specialized diet, making them more interesting for our purpose.

We shall begin with a leaf-mining representative of the family Buprestidae, *Trachys pygmaea* F., which develops within the leaves of *Althaea officinalis* L. belonging to the mallow family. The larvae of Buprestidae, as is well known, live for the most part in cases within the branches or big roots of various trees and shrubs; therefore they are xylophagous and exhibit a flattened body, a very strong prognathous or subprognathous head capsule, deeply enclosed by the prothorax, which is rather broad and gives to the insect a clubbed appearance. Ocelli and legs are absent. The modifications undergone by the larva of *Trachys pygmaea* F. (we compare it with the larva of *Capnodis tenebrionis* L. in order to have a reference) consist mainly of a widening of the body segments and therefore the loss of the clublike aspect; the reduction of the head size in comparison with the thorax; much greater enlargement of its free portion (the outer part); the disintegration of the head, and the rather less sclerotization of its inner part; the presence of ocelli, a greater development of the antennae and their supply of sensillae; a fine sculpture of the segments of the integument and the presence in them of ambulacral areas and little sclerotized patches. All the above is obviously in correlation with a microhabitat that is larger, softer, and clearer than that represented by the dark, narrow, rigid, and hard-walled galleries bored in the wood, and with the different feeding. The reappearance of ocelli, that is, organs lost not in a stage or phase preceding the larval ontogenesis, but in almost all the representatives of a family

which from time immemorial has adapted itself to living in a peculiar environment, is particularly important.

Among the Chrysomelidae with phyllophagous larvae, I have studied several species of Halticinae, Orsodacninae, and Hispinae. For the necessary comparisons I have taken into account a halticinus, whose larva is rhizophagous and hypogeous. Among the phyllophagous Halticinae, *Dibolia femoralis* Redtb. and *Sphaeroderma rubidum* Graëlls, respectively miners of sage and *Cynara* leaves, exhibit the most modified larvae: body moderately flattened with reduced trichotaxis, head capsule prognathous, posteriorly prolonged by laminar dorsal processes, which penetrate into the thorax; tendency of the antennae to be displaced dorsally and anteriorly; enlargement of the labium, a rich supply of bristles and bristly processes in several portions of the mouth parts; expansion of the maxillolabial complex and tendency of some sclerites to coalesce, of the ligula to develop, of the labial palpi to undergo involution; a slight indication of formation of ambulacral areae; a constant presence of the more or less regularly formed thoracic legs, etc.

The larvae of *Phyllotreta nemorum* L., which mine leaves of *Erysimum*, appear less modified; those of *Aphthona cyparissae* Koch, living on the roots of *Euphorbia*, are nearly normal.

The modifications undergone by the larvae of Hispinae, *Hispa testacea* L. (miners of the leaves of *Cistus*) and *Hispella atra* L. (miners of the leaves of *Agropyrum*), follow, though with some deviations, the same course as the larvae of the most specialized Halticinae.

The larva of the Orsodacninus, *Zeugophora subspinosa* F., developing within the *Populus* leaves, conspicuously and differently transformed, exhibits modifications resembling in a certain way those of the first phase larvae of Lepidoptera Phyllocnistidae and Gracilariidae: body flattened and anteriorly enlarged; head capsule flattened, prognathous, prolonged backwardly by two dorsal and lateral processes penetrating into the thorax, which has two strong apodemata; labium very large with a thick suite of enormous spatulate bristles; mandibles elongated and depressed; maxillae with large sclerotized stipites and cardines, pushed back and drawn near each other beyond the labium, which is involute and exhibits contiguous, subatrophied labial palpi, furnished also with spatuliform bristles. For these particular conditions the maxillary complex, which has shifted and modified, is placed under the labrum, forming with it two pinnate plates, between which the mandibles move. The legs are absent. Ambulacral arrangements

are present in the thorax and abdomen. The development is euholometabolic.

In the very large family Curculionidae the larvae are, as is known, apodous, and generally cyrtosomatic. Almost all, moreover, develop endophytically; therefore I have selected ectophytic or leaf-mining forms.

Among the open feeders (*sensu lato*) I have examined some Meccininae belonging to the genus *Cionus* Clairv. (*hortulanus* Geoffr., *scrophulariae* L., *olens* F.). The clearly ectophytic larvae of the first two species do not exhibit, as was to be expected, very remarkable features except the presence of pseudopodia in the first eight segments and the fact that they cover their own bodies with a kind of liquid protective cloak. But if we consider the larvae of the third species, which have a somewhat specialized behavior, we may point out some interesting facts. These larvae, even though really living ectophytically on the very woolly leaves of several *Verbascum*, have the odd habit of excavating a kind of gallery in the woolliness, that is, a kind of mine of a new type—actually, a pseudomine—and keeping the head in the horizontal plane while shifting it sidewise and anteroposteriorly. They exhibit some peculiar characteristics of the mining larvae: head capsule flattened, hypognathous, but with a tendency to prognathism, very much enlarged and furnished with two curious sublateral sclerites, which, joined as they are to the posterolateral edges of the dorsal surface of the head capsule by means of a narrow membranula, take the place of the laminar processes repeatedly mentioned in regard to the mining larvae of several orders of insects. Moreover, on the ventral face two conspicuous quadrangular expansions, joining tentorial pons and hypostomal laminae, contribute to close the head capsule before the foramen magnum.

Among the leaf-mining Curculionidae we must consider the weevils belonging to the genus *Rhynchaenus* Clairv., whose larvae bore rather high and narrow laminar mines, at least in the first period of their lives. They exhibit a body moderately flattened; head capsule subprognathous, flattened, caudad prolonged by two dorsal lateral plates attenuated abruptly in the distal part and here enlarged like a club, between which a prolongation of the medial longitudinal apodeme of the epicranium conspicuously juts like a rigid staff. On the lower surface the hypostomal laminae, expanded in large plates which converge almost to the point of meeting, tend in such a way to close the head capsule before the foramen magnum. The cranial walls are strengthened by strong apodemata; the integument of the antennae and the maxillolabial complex is sclerotized.

Of course, the larvae of Coleoptera with a specialized diet (miners included) present less plasticity than Hymenoptera Tenthredinidae, and more than Lepidoptera, but as a rule their modifications have a similar tendency.

III. LARVAE OF PARASITIC COLEOPTERA HYPERMETABOLA (RHIPIPHORIDAE)

The Rhipiphoridae are protelic parasitic Coleoptera for the most part hypermetabolous and generally developing at the expense of Hymenoptera and Blattoidea (the Pelecotomini are thought to live at the expense of xylophagous larvae and to be euholometabolous). The hypermetabolous forms exhibit an asynchronous larval dimorphism, viz, two very different larval phases following each other in order of time and strictly related to the "necessities" (let us call them so for the sake of clarity) and complications of their life cycle.

In order to discuss them, we shall refer to the Rhipiphorini (making use of what I learned in 1936 regarding *Macrosiagon ferrugineum flabellatum* F., fully confirmed in 1952 by the North American biologists Linsley, MacSwain, and Smith on *Rhipiphorus smithi* Linsl. and MacSw.) and Rhipidiini (making use of the recent work of Cl. Besuchet (1956) on *Rhipidius quadriceps* Ab.).

Macrosiagon ferrugineum develops at the expense of a large solitary vespid eumenid, *Rhynchium oculatum* Spin., which builds its nest in the reeds of *Arundo donax* and massively nourishes its offspring with the entire caterpillars previously paralyzed.

The coleopteran female (dwarf in respect to *Rhynchium*, a thin, weaponless insect) to enable her larvae to reach the host shelter chooses an indirect way and lays a large number of eggs on the plants on which the hymenopteran usually lives and feeds. After hatching, the larvae (of the first phase) take care of attaching themselves to the foraging *Rhynchium* individuals, and some of them succeed in having themselves carried to the nest of the destined victim. Having reached this place, the larva waits until the host larva comes up to feed, then penetrates inside the host, stays for some time in the superficial sinus of its body cavity, and finally sinks.

During the endozoic life, the larva feeds on the victim's humors, swelling enormously; afterward it makes its way through the host integument, moults, sheds the old covering to plug in some way the wound in order to prevent a too severe hemorrhage and, transformed into a larva of the second phase which will live as an ectophagan, comes out.

How are the two phases of larvae formed? The larva of the first phase in its free stage (jeune) is an oligopodous (hexapod), campo-deiform, macrocephalous larva, with pigmented, sclerotized integuments; it resembles the so-called "triungulin" of the Meloidae (other Coleoptera, which undergo hypermetamorphosis, also parasites of Hymenoptera Aculeata or of the egg clusters of Orthoptera Caelifera). Its large head is prognathous and partly disintegrated; with rather long antennae, five ocelli on each side; the mouth parts are fitted for biting with large mandibles; legs with lanceolate, membranous pretarsi; there are nine pairs of stigmata. During its endophagous stage (replete) it does not exhibit important modifications of any kind, but has swollen until it looks like a little sausage.

The larva of the second phase, enormously different from that of the first phase, is a pseudopolypod, pseudoeruciform, microcephalous, anophthalmous larva with membranous, depigmented integument; its thoracic limbs are transformed into rough, digitate processes; in the abdomen there are 8 pairs of pseudopodia; thoracic and abdominal segments armed with about 60 large subconical laterodorsal protuberances, which give it a monstrous look. The head capsule is small, slightly sclerotized and subhypognathous; the antennae are cupulate; there are no ocelli; the mouth parts are peculiarly made, fitted for tearing and sucking, the upper and lower lips (partim) form a sort of membranous beak and the mandibles move obliquely without crossing, with the tips turned out; stigmata, shaped like a truncate cone, are supported by short prominences.

A life cycle like that of *Macrosiagon* and other Rhipiphoridae with a protelic parasitism performed at the expense of such powerful, industrious Hymenoptera had of course the possibility of developing in a simpler way, with fewer difficulties and hazards. This is shown by the Cleridae (Coleoptera) belonging to the genus *Trichodes* Herbst, also parasites of Hymenoptera Aculeata; they lay eggs near the nests of the victim where the considerably modified larva reaches the host pedotrophic cell by its own efforts and manages by itself to achieve its objective. Therefore, as regards Rhipiphoridae, it is not possible to speak of behavior related to necessity. We can only admit that the life cycle of a coleopteran such as that of *Macrosiagon* (and allies), beginning with the female habit of laying eggs far from the host nest, required an agile, flexible, sheltered larva, whose mandibles had a powerful hold and whose pretarsi were fit for helping these gnathites to keep this hold, resisting adversities on all sides, supported in the attainment of its purpose by a considerable fecundity of the female,

thus providing "a priori" for the inevitable failure of the efforts of a large number of individuals. Furthermore it can be admitted that this larva, having achieved its aim, could have no more reason for keeping its features. Now we cannot deny, in a larva of the caterpillar type, having the thoracic legs transformed into membranous pseudolegs and the abdominal pseudopodes fitted for attaching an hectophagous larva to the victim's body, that the tracheal spiracles emerging on prominences prevent the haemolymph, running from the voluminous body of the victim, from penetrating into the tracheae, or that the mouth parts fitted for tearing and sucking are correlated with an haemato-phagous diet. It is obvious, however, that from another point of view, we are in the presence of a rather odd plasticity, which seemingly has no appreciable meaning in the light of what we know at present.

Rhipidius quadriceps Ab. lives on the preimaginal stages of several species of Blattoidea belonging to the genus *Ectobius* Steph. The female lays eggs on the bark of plants. The larva of the first phase does not wait for the host, but goes and looks for it without delay. Having reached it, the larva attacks the intersegmental corium, into which it wedges its head and a portion of its thorax. After 2 to 3 weeks a new very odd larval instar, which in a special way is injected into the victim's body cavity, issues from this larva which has practically remained ectozoan. There it passes the summer, fall, and winter in diapause (growing little or not at all). In April it is transformed (through a kind of transition instar which feeds actively) into the last larval phase, which remains within the host up to the moment of undergoing metamorphosis; then it emerges and pupates outside. The *Rhipidius* larva of the first phase (triungulinum) is like the larva of the Rhipiphorini. The larva of the last phase is very different from that of this subfamily; its mouth parts are formed by only one pair of appendages, considered to be maxillary palpi; the mouth is physiologically closed and there are three pairs of well-developed legs (it must walk to where it will pupate). Of the two intermediate stages, the interesting instar is the one injected into the victim's body cavity by the triungulinum; this is an apodous, indistinctly jointed form with a membranous integument, without antennae, mouth parts (although it is not astomous), and stigmata. In the cycle it takes the place of the replete form of the Rhipiphorini's triungulin. It is clear that the different cycles and behaviors of the various preimaginal instars, except the triungulins that have similar tasks, exhibit strongly differentiated structures.

IV. LARVAE OF HYMENOPTERA SYMPHYTA (CEPHIDAE,
TENTHREDINIDAE)

Also among Hymenoptera Symphyta, there are many species whose larvae develop within plants and many ectophytic species which exhibit behaviors interesting in the light of the facts under discussion.

It is well known that the larvae of these Hymenoptera, for the most part phytophagous and of generalized type, are polypod, cruciform larvae like those of Lepidoptera, from which they differ in the three following characteristics: A single lateral ocellus, the presence of abdominal legs also on the second urite, and the absence of the particular thricotaxis characteristic of the caterpillars. Now we shall examine particularly some of those having a specialized diet and observe their behaviors.

The larvae of the tenthredinid hoplocampinous *Caliroa limacina* Retz., devour ectophytically the upper epidermis and the parenchyma of the leaves of the pear and other trees, passing their lives in contact with flat surfaces. The body is characteristically shaped: flattened on the ventral side, convex on the dorsal side, gibbous in the anterior portion. The head capsule is nearly invisible from the upper side, because it is not only turned downward, but also recurved backward and therefore strongly metagnathous; ocelli are displaced dorsally and the antennae conspicuous and well supplied with large sensillae, the thorax has the prosternum very reduced in length with a membranous integument and also two very conspicuous fingerlike glandular prominences, which, when the insect feeds, converge forward and come into contact with the labrum. The legs are exceptionally shaped, having an enormous coxa, a stout femur-trochanter and tibiotarsus, and a large claw. Obviously these modifications are correlated with the larval habit of feeding on the surface, but not on the edges of the leaf. To the question whether these modifications were necessary, we should answer negatively. However, we cannot assert, at least for some of them, that there may not be some moderate use and above all an intimate correlation with the particular insect behavior.

On the other hand, the larvae of the cephid hartiginous *Janus compressus* F. bore centripetal galleries within the twigs of pear trees, pushing the gnawed substance behind them, and they are very curiously formed. In fact the head capsule of the full-grown larva is clearly, although only slightly, asymmetrical as a result of a moderate clockwise rotation of its anterior portion following the lowering of the right side of this portion. Clear signs of it are the behavior of the anteclypeus, the displacement of the invagination pit belonging to the

anterior arms of the tentorium, their different length and position, the oblique articulation of the labrum and different direction of its sclerotized posterior processes, the absence of lanceolate bristles on the left side of the epipharynx and their presence on the right side, though abraded by use, the erosion of the teeth of the right mandible, etc. The thoracic legs are transformed into subpyriform organs, without distinction of the various parts; the abdominal legs are absent, except in the 10th urite (which protrudes dorsally and backwardly in an irregular, sclerotized, pigmented, toothed, hairy process), where they are, however, vestigial. This condition is correlated with peculiar procedures in the act of gnawing wood. As a matter of fact the boring larva turns its head, advancing by clockwise windings like the curls of a spire. It is noteworthy that in the new-born and still inactive larva the labrum, anteclypeus, and tentorium are asymmetrical; the lanceolate palatine bristles, present and entire in the right side, are absent in the left side. Similar conditions occur in other larvae of wood-feeding Hymenoptera Symphyta, as for instance those of the large Sirecidae.

Several Tenthredinidae Phyllostominae and Blennocampinae belonging to the genera *Phyllostoma* Fall., *Pelmatopus* Hart., *Metallus* Farb., *Fenusa* Leach, *Fenella* Westw., and others are leaf miners in the larval stage, but generally live within the parenchyma (seldom near one of the two epidermic surfaces), usually bore gall mines and are euholometabolous (here and there we observe a rare exception). Some of these, as the larvae of *Pelmatopus mentiens* C.G., which may be found in the leaves of the buttercup (*Ranunculus*), appear little or not at all modified. We may observe only the forward displacement of ocelli and the reduction in length of the antennae which exhibit joints heaped one on another in a special way. In the other above-mentioned genera the modifications occur approximately on the same plane; the body is moderately flattened; the head capsule is prognathous, more or less projecting on the sides, posteriorly attenuated and prolonged in a kind of lamina, which penetrates into the thorax. The invagination pits of the anterior arms of the tentorium are more or less considerably displaced caudad. Ocelli are displaced a little dorsally and somewhat anteriorly. The labrum is broad, sublaminar, and shows ventrally the epipharynx with conspicuous and lanceolate bristles. In the mouth the mandibles are depressed but not laminar, and the parts forming the maxillolabial complex are well differentiated, the integument of its lower surface is almost completely sclerotized, but it does not coalesce with the head capsule as in the

previously examined Lepidoptera, though it functions in a like manner. The thorax has very interesting features. Each of its three segments has legs, which, however, are variously formed and localized. Indeed some legs (for instance in *Fenusa ulmi* Sund.) consist of coxa, trochanter-femur, tibiotarsus, and a large claw, and are little moved laterally outward; others (for instance in *Fenella nigrita* Westw.) consist of the same but noticeably smaller parts and are more displaced outward; others, moreover (for instance in *Phyllotoma aceris* McLachl. and *P. microcephala* Kl.), are reduced to biarticulate, clawless stumps and are so much displaced outward as to become nonfunctional at the sides of the segments. In all these species, therefore, the thoracic legs have a tendency to be set toward the sides of the somites and can reach their edges. Where their natural seat was, two "ambulacral areas" have been formed as two vicarious organs. Instead the abdominal legs have undergone an involutive process and have been transformed into simple prominences of little importance. The comparison between the behavior of the Tenthredinidae mining larvae and that of the lepidopteran larvae having similar habits is very interesting. We find the same tendency in the modifications undergone by these insects, but in the former the phenomenon is kept within more moderate limits; this fact, nevertheless, has to be considered in relation also to their manifest plasticity and to the fact that no known larva of a tenthredinid bores flattened mines in only a single layer of cells of the leaf blade. Also in the Tenthredinidae the thoracic and abdominal legs tend to undergo involution and disappear, but here we are in the presence of a more or less marked displacement with consequent uselessness of organs (thoracic legs) and their replacement with new organs, probably better fitted to cope with the resistance of the medium in which the insect lives and feeds. No morphological "adaptation" can show better than this does the course followed by it in its manifestations or the ways of its determination and finally its biological meaning.

V. LARVAE OF SOCIAL HYMENOPTERA APOCRITA (VESPIDAE, APIDAE)

It is well known that the larvae of the social Vespidae are nourished, at least after a few days from their hatching, upon bits of crushed insects brought to the nest by the nurses, which distribute and subdivide them among the progeny; thus the larvae receive the pabulum ventrally behind the head and may consume it at their ease by folding their heads under the thorax. Equally well known is the extraordinary

importance in the insect communities of the practice of trophallaxis, or mutual exchange of food (among the Vespidae the larvae give up the secretion of their labial glands to the nurses), and also the existence among the Vespidae of naked or gymnodomous nests (that is, with combs not protected by envelopes) and calyptodomous nests (those having the envelopes).

In the larvae of the Polistini (of *Polistes* Latr.), which form primitive communities and live in gymnodomous nests, the 1st urite not only is longer than the two following urites, but projects on the ventral surface like a moderately developed hump ("trophothylax," sensu Wheeler). The considerably pigmented cranial integument is well provided with rather long hairs, and the very remarkable maxillo-labial complex is almost as wide as the head capsule, which conspicuously projects on the ventral face of the body (owing to the great development of the postlabium) and has also a pigmented integument. The larvae of the Vespini (for instance *Vespula* Thoms., *Dolichovespula* Rohw., and others), which live in more highly evolved communities and in calyptodomous nests, have the 2d traylike urite remarkably projecting on the under side ("tropholopade," sensu Grandi), the cranial integument not pigmented, its cuticle provided with a small number of microscopic hairs, and the maxillolabial complex kept within moderate limits (owing also to the shortness of the postlabium) and not pigmented (palpi excluded). In both, the so-called "spinneret" (an external organ placed anteriorly in the labium, where it is joined to the prepharynx, and at the tip of which the duct of the salivary or labial glands opens), which in the solitary Vespidae has the shape of a small transverse, more or less sclerotized lamina, looks like a double membranous lip which is more or less distinctly trilobate and rich in filiform tegumental outgrowths. "Trophothylax" and "tropholopade" serve as a support for the alimentary bolus which, sticky as it is, adheres to it even though the comb openings are turned downward and therefore the larva is downheaded.

The spinneret structure seems to be well suited to the trophallactic function. Finally the head of the Polistini is seemingly modified to form a kind of cover for the comb cell, in correlation with the fact that in the nest not covered by protective envelopes the larva is in direct contact with the external environment.

The honey-bee communities are considered to be among the highest insect colonies. They present such an advanced way of nursing their offspring that larvae are not compelled to take care of themselves or to make any effort to take food. Now, these larvae, as far as is known, are the only larvae of Hymenoptera Aculeata exhibiting (ac-

ording to my findings of 1934) clear involucional features such as the disappearance of the antennal sensillae, general reduction of the hairs and sensillae of the head capsule and of its appendages in number and length, transformation of the mandibles into little sclerotized subconic organs, a reduced differentiation of the maxillae and sclerotized regions of the palatine and prepharyngeal integument, and so on.

VI. ADULTS OF HYMENOPTERA CHALCIDOIDEA DEVELOPING IN THE RECEPTACLES OF *FICUS* L. (IDARNIDAE-AGAONIDAE)

The embryonic and postembryonic development of these Terebrantia, at least as far as is known today, occurs within the pistillate galligenous flowers of the receptacles of Moraceae belonging to the genus *Ficus* L. The Agaoninae cause the parthenogenetic formation of the endosperm (on which their larvae will feed) in the host-plant flowers, wherein they put at the same time with the egg some drops of the secretion of a gland attached to the female genital terebra. The behavior of the Sycophaginae is unknown. As regards the Idarnidae, the facts I discovered concerning the genus *Philotrypesis* Först. have made it clear that the development of these Chalcididae depends indirectly on the preceding intervention of an agaoninuous.⁴

The females, after eclosion in the collective fruits (i.e., galls) where they developed, may pass their imaginal lives: (a) completely outside the receptacles in the species which lay eggs outside the inflorescences after they have left, as far as is known, through the ostiolar canal (almost all Idarninae); (b) partly outside, from the time of their coming out of the ripe collective fruits through the ostiolar canal, straining its soft phyllomes, or through the receptacle walls, to the time of going into the successive inflorescences, again through the ostiolar canal, wedging themselves into the resistant, turgid, imbricated phyllomes and partly within the receptacles, from this time up to death, for the species, which in order to lay eggs must penetrate into inflorescences, where they will die after oviposition (Agaoninae).

The males, after their eclosion which occurs likewise within the collective fruits (i.e., the galls) where they developed, may spend their imaginal lives: (a) outside the receptacles, after emerging as do the females through the ostioles; but these homeomorphic winged forms constitute only a small minority (some Idarninae and Sycophaginae);

⁴ What I have found since 1921 in regard to this matter has recently been confirmed by K. J. Joseph (1956-1957).

(b) completely or almost completely in the inflorescences for the heteromorphic, apterous or subapterous forms constituting the great majority (most of the Agaoninae and Idarninae).

The females belonging to group (a) present no modifications, but a more or less exceptional development of the terebra, and also sometimes, in connection with this development and therefore with the oviposition, peculiar deformations of the last abdominal segments or other regions of the gaster.

The females belonging to group (b) show more or less greatly complicated modifications of several regions of the body and also of the segmental and tegumental appendages. Of such modifications some are common to all the members representing the taxonomic groups under consideration, others are characteristic of particular genera or species. However, both appear related to the work which females have to do to penetrate into the inflorescences. Nevertheless, some of them are unnecessary, except such as are likely to aid the female during her efforts. (We remember, for instance, the flattening, disintegration, and consequent deformability of the head capsule; the peculiar conformation of the first three joints of the antennae and the recurved bristles, which are often found on the 2d toothlike antennomere, the formation of a new organ, namely, the particular mandibular process having the shape of a broad transversely carinate, serrate appendage, the localization of series or complexes of small recurved odontoid processes in various regions and appendages of the body, the strengthening of the fore and hind legs, the shortening of their tibiae and their rich outfit of spiniform or odontoid bristles, the transformation of the maxillary stipites into sclerotized plates horizontally arranged so as to form a kind of chisel, and so on.) Others seem to be the result of involution or rudimentation of organs or appendages (atrophy of the labrum, more or less advanced reduction of the maxillae with atrophy or disappearance of the maxillary palpi, a more or less advanced rudimentation of the labium and disappearance of the labial palpi, reduction in number or disappearance of ocelli, a more or less advanced reduction of the distal parts of the fore-wing venulation, etc.); others do not seem to have, at least in our opinion, any particular functional meaning (a more or less pronounced and sometimes hypertelic elongation of the head capsule, orientation in subvertical direction of the mandibles, their transformation into strong, rather complicated organs, the formation of enormous, monstrous new organs such as the fore tibial laminae in the genus *Sycoecus* Waterst., in

order to differentiate there the usual series of backward odontoid microprocesses, etc.).⁵

The males belonging to group (a) (homeomorphic) are not modified. The males belonging to group (b) (heteromorphic) are highly modified and sometimes so much so as to lose even some important characteristics of the order and even of the class to which they belong. Also, some of the modifications undergone are common to all the members of the various taxonomic groups; others pertain only to certain genera or species. Both, however, seem to be in connection with determinate functions (opening of their own galls from inside, and those of the females from outside, particular ways of mating which compel the males to grasp at the galls or penetrate into them, etc.), or the microhabitat (the inside of the receptacles), in which they remain from the time of eclosion up to death—they live and die without ever knowing the external world and sunlight. Among these modifications (as we have previously pointed out in regard to the females) we find some which seem to be of moderate use for the functions the male has to perform (for instance we remember the shortening, oligomery, and fusion of antennal joints and the concentration of their sensilla in the distal end of the last antennomere or of the last group of antennomeres; the strengthening of the mandibles; the particular modifications of the thorax and abdomen), solenogastria, the particular shape of the 9th urite; the strengthening of the fore and hind legs, etc.); some of these characters seem to be the result of the involution or rudimentation of certain organs (atrophy of the labrum, reduction or atrophy of the maxillolabial complex; reduction or disappearance of the intergnathal cavity and its outer opening, which induces the formation of "astomous" and "aphagous" forms; involution, atrophy or disappearance of the middle legs, which induces the formation of "tetrapod" forms; involution, atrophy, or disappearance of one pair of wings which causes the formation of "dipterous" forms, or of all four wings, which gives rise to "apterous" forms; disappearance of the cerci, etc.); some, which conversely appear as hypertelic modifications (a rare monstrous hypertrophy of the antennal scape, or of the first or last tarsomere; abnormal development of the head capsule and mandibles, etc.); some which, though included at least in part in the two last groups, nevertheless seem to be related to the changes undergone by the organs and are considered in the first group (antennal and tarsal oligomery; malformations of some parts of the legs and

⁵ What is affirmed above is on the basis of what we know today, and actually we know very little.

anchylosis of the femorotibial, tibiotarsal, and intertarsomeral articulations; more or less advanced fusions of thoracic and propodeal nota; decomposition of the head capsule and pronotum into sclerites secondarily joined one to another, etc.); some which are clearly in connection, even indirectly, with the special microhabitat where the insects live (tegumental depigmentation; involution and disappearance of the eyes and ocelli, etc.); finally, some which, even in this case, do not seem to have any functional purpose (more or less numerous and large posterior spiniform bristles on the upper region of the head; particular adaptation of the antennae within fossae or really within dorsally open or closed cranial pockets, etc.).

Besides, the heteromorphic males of some Idarninae sometimes exhibit remarkable continuous or discontinuous, megetic and morphological individual variability.

It is well to remember, too, that Sycophaginae, the females of which, as far as known, penetrate into the fig-host inflorescences to lay eggs, wedging with difficulty like Agaoninae into the phyllomes obstructing the ostiolar canal of the receptacles, are less specialized than the Agaoninae. These females indeed (we know very little about the males) are rather less modified than Agaoninae and show a very variable structure.

Furthermore, we may say finally that the behavior of some species proves that a life cycle based on oviposition within the pistillate flowers of *Ficus* (at least of some *Ficus*), with the embryonic and postembryonic development of the insect within the galls produced by them, may be normally accomplished without occurrence of any modification in the forms which have adapted themselves to living in such a habitat.

VII. ADULTS OF PARASITIC HYMENOPTERA VESPOIDEA (CHRYSIDIDAE)

The Chrysididae are Hymenoptera Aculeata that develop at the expense of other Hymenoptera, or less frequently of insects belonging to other orders. We know some which are parasites of larvae of Tenthredinidae (Cleptinae); some that emerge from eggs of Phasmoidea (Amiseginae); and some that live at the expense of Hymenoptera Aculeata and larvae of Lepidoptera (Chrysidinae).⁶ The females, for oviposition, penetrate into the pedotrophic nests of the victim, opening the cocoon if necessary with their mandibles. Their larvae devour the host larva or the preys stored by the latter for its progeny, or both at the same time. In some cases, however, other

⁶ See Krombein, K. V. (1956).

victims are preferred, and Lepidoptera Limacodidae are sacrificed. The female Chrysidid seeks the cocooned caterpillars, breaks the protective shell with her mandibles, inserts into it the extroflexible tubular part of the gaster, stings and paralyzes the larva, lays an egg on it, and then closes the opening by making use of the scraped matter mixed with secretion of her salivary glands.

The Hymenoptera here discussed show a characteristic facies; they are of a brilliant coloration with a very sclerotized integument.

The Chrysidinae are well known also for their thanatotic reflexes. In akinesia they turn the forebody under the lower surface of the gaster, rolling themselves into a ball.

Before my researches (1943), the Cleptinae were considered to have a functioning aculeus, and the Chrysidinae a reduced or at least an inactive and involute aculeus, with the exception of those which are parasites of Lepidoptera, and some exotic forms.

Now we shall examine the structure of the female gaster. Some Chrysidinae (*Chrysis* L.) and the Cleptinae are solenogastric. In the former the urites externally visible in a state of rest are three (2d, 3d, 4th); those invisible and capable of extroflexion are five (5th to 9th); in the latter the visible urites are four (2d to 5th) and those extroflexible are four also (6th to 9th). The telescopically evaginable portion of these gasters when completely extended is two or more times as long as the fore portion and presents an exceptional structure; the 7th urosternum (which, as in all Hymenoptera, really forms the subgenital plate) in correlation with the large prolongation of the caudal part of the gaster, displaced from its normal position, has slipped backward, leaving the 7th tergum without an opposed sternum and placed under the 8th urotergum, with which it has thus formed a strange heterogeneous segment. The ovipositor is quite well developed, but its "outer plates" and cranial part of the valvae of the 3d pair are long and thin, resembling the ovipositor of Terebrantia. Nevertheless, the valvae of the 1st and 3d pairs form what is properly called a sting, the sheath of which, however, is rather short and only about a third of the caudal part of the valvae, at the expense of which it has been formed. Other Chrysidinae studied by me (for instance, *Hedychrum* Latr., *Hedychridium* Ab.) are instead pseudosolenogastric. In fact their 5th to 8th urites form but a little evident complex, which when fully extended does not exceed in length the fore part of the gaster; the 6th to the 8th urites are a little longer than wide. Here the 7th urosternum is below both the 7th and the 8th urotergum. In all the Chrysidinae examined by me, the 2d to 4th urosterna appear

flattened and disintegrated, that is, crossed by sutures running in different directions which permit them to bend lengthwise as well as transversally; in the nonthanatotic Cleptinae the urosterna are undivided and a little convex.

The lack of more thorough knowledge on the ethology of these Hymenoptera does not permit me to discuss objectively what I had formerly learned. However, it may be observed that: (1) in regard to the thanatosis of the Chrysidinae, the disintegration of the 2d to 4th urosterna permits a very intimate mutual adaptation between forebody and lower surface of the gaster (obviously this does not correspond to a necessity, nor is it of use in rolling up); (2) with regard to the solenogastria, the ability to lengthen telescopically the urites nearer to the hind end of the gaster is clearly correlated with oviposition within closed cells or cocoons, but even here it is not at all a necessary condition, because the point to be reached may be attained without a gaster of this type, as is shown by the pseudosolenogastric Chrysididae.

CONCLUSIONS

Data could be multiplied and collected from different fields, but from what has been summarized above and from the coordination of the observations described, it is possible to come to the conclusions here summed up in 18 units.

1. The modifications undergone by the organisms studied by me (insects of several families belonging to three orders of Holometabola in both imaginal and preimaginal stages) are always connected with the function which the organ or the group of organs concerned has to perform, and on the whole with the work the organism has to do in the particular environment in which it lives.

2. These modifications can be collected into about five classes: (A) involutions, rudimentations, or disappearance of organs or portions of organs; (B) abnormal (hypertelic) developments of organs or portions of organs; (C) displacements of organs; (D) transformation of organs or portions of organs; (E) development of new parts in preexisting organs and also of new organs.

3. When it is a question of new organs, we are always in the presence of more or less advanced differentiations of determined somatic regions, which organize into special forms what elsewhere are characteristic of the same regions.

4. The modifications undergone by a species (or by a higher taxonomic group) are generally numerous and complicated and often functionally coordinated, so that they may involve several organs or

portions of organs, each of which has, of course, its own function related to the functions of others, within the limits of the general behavior.

5. The modifications undergone by a group of organs in connection with a particular function often affect different organs of the same complex or different portions of the same organ in different species, genera, families, and orders.

6. The modifications affecting the same organ may be different (but all coordinated with the same function) and more or less advanced in a determinated sense in the various species of a genus (or a higher taxonomic group).

7. The modifications of organs or somatic regions may concern only one half of them (antimeric) and so determine an asymmetric structure.

8. An organ so modified as to acquire an impractical form and size—that is, a hypertelic organ—may exhibit other corrective modifications which seem to attenuate the functional inconveniences caused by its abnormal structure.

9. An organ that has disappeared during a phase of the postembryonic development may appear again in a second phase of the same development and therefore of the ontogeny.

10. An organ that has disappeared during postembryonic stages of a whole family, evolving in a particular environment, may be found in the postembryonic stages of some representatives of the same family living (probably owing to a secondary adaptation) in a different environment.

11. The modifications undergone by the organisms studied by me, which as stated before are always connected with the function the organs have to perform, generally do not seem to be necessary, often not even useful,⁷ sometimes even a hindrance (if not disgenic).

12. In fact, species belonging to the same taxonomic group (for instance to the same family) may live and develop in environments like those inhabited by the modified forms, and perform basically similar functions, but conversely may have undergone no modifications.

13. It even happens that in a hypermetamorphic species two types of larvae, the first highly modified, the second quite unmodified (which, however, bore diversely shaped mines and feed in a different way) follow each other in succession during the postembryonic development and in the same microhabitat.

14. There are species (hypermetamorphic and parasitic) that have

⁷ As far as known at present.

an irregular and complicated life cycle; their complications, however, do not seem to be justified by any necessity (as is shown by the existence of other species belonging to the same order which achieve their aim in a much simpler way). These species, too, exhibit two very different larval phases, but living in different environments and performing different functions and activities.

15. There are species in which we can observe slightly marked modifications related to particular organs for particular functions in particular environmental conditions; these modifications can be understood as the expression of a limited organism plasticity, or as an initial stage of the modifying process, or also, if we prefer, as the combined result of the two possibilities.

16. There are species in which the modifications of an organ related to the functions to be performed in particular environmental conditions appear even, though little marked, when the particular characteristics of that biotopos requiring or permitting that behavior are scarcely marked.

17. There are species in which we can point out a behavior that shows us the process undergone by an organ, a group of organs, or a somatic region, in order to change.

18. All the modifications considered seem to be included in a class whose representatives have characteristics like those referable to the processes of so-called esogenous adaptation, but which, however, are hereditary and, therefore, susceptible of manifesting themselves in an independent way.

EXPLANATION OF PLATES

PLATE I

Gracilaria latifoliella Mill. 1, larva of the 1st phase, dorsal view of the head (*A*, antennae; *L*, labrum). 2, idem, ventral view (*A*, antennae; *I*, prelabium; *M*, maxillae; *S*, postlabium). 3, larva of aphagous phase, head, dorsal view (*A*, antennae; *L*, labrum; *N*, mandibles; *Q*, labial palpi; *R*, prepharynx; *T*, tentorium). 4, idem, ventral view (*F*, spinneret; *I*, prelabium; *M*, maxillae; *P*, maxillary palpi; *S*, postlabium). 5, portion of the head capsule with a slight indication of mandible. 6, anterior portion of 4, much more magnified.

Gracilaria stigmatella F., larva of the 1st phase. 7, head, dorsal view (the same lettering). 8, idem, ventral view (*O*, anterior portion of the maxilla), 9, left antenna, dorsal view. 10, anterior portion of 7, much more magnified (*Cl*, clypeus). 11, mandible, ventral view. 12, anterior portion of 8, more magnified.

Phyllocnistis suffusella Zell., larva of the 1st phase. 13, mandible.

PLATE 2

1, *Capnodis tenebrionis* L., larva, dorsal view. 2, idem, head, dorsal view. Gnathites are not drawn. (*A*, antennae; *C*, anteclypeus; *CA*, articular cavities for the mandibles; *CM*, dorsal condyle for the articulation of the mandibles; *L*, labrum; *P*, peristoma.) 3, 4, *Trachys pygmaea* F., larva, dorsal and ventral views. 5, idem, head, dorsal view. Gnathites are not drawn. (*A*, antennae; *C*, anteclypeus; *E*, epistomal apodeme; *L*, labrum; *O*, ocelli; *SD*, diverging sutures; *SE*, epistomal suture.) 6, *Aphthona cyparissae* Koch, larva, head, dorsal view. Gnathites are not drawn. 7, *Phyllotreta nemorum* L., larva, head, thorax, and 1st urite, three-quarter view (*S*, tracheal spiracles). 8, idem, head (*A*, antennae; *M*, mandibles; *R*, diverging sutures; *Z*, dorsolateral membranous regions of the head capsule). 9, idem, anterior portion of the head capsule (*G*, postclypeus; *H*, anteclypeus).

PLATE 3

1, 2, *Dibolia femoralis* Redbt., larva, head, dorsal and ventral views. Gnathites are not drawn. (*T*, fore arms of the tentorium broken on purpose.) 3, *Sphaeroderma rubidum* Gräells., larva, lateral view. 4, 5, idem, head, dorsal and ventral views. In the latter the mandibles are broken on purpose.

PLATE 4

1, *Hispella atra* L., full-grown larva, dorsal view. 2, idem, head, dorsal view. 3, idem, newborn larva. 4, *Hispa testacea* L., full-grown larva, dorsal view. 5, head, dorsal view. Gnathites are not drawn. 6, idem, maxillolabial complex. 7, idem, portions of the metathorax and 1st urite, ventral view. 8, idem, median portion of the 3d urotergum.

PLATE 5

1, *Dibolia femoralis* Redbt., larva, maxillolabial complex (*P*, labial palpi). 2, *Sphaeroderma rubidum* Gräells., larva, portion of the maxillolabial complex. 3, 4, *Zeugophora subspinosa* F., larva, head, dorsal and ventral views. Mandibles are not drawn. (*C*, maxillary cardines; *D*, concavity for the ventral articulation of the mandibles; *L*, labium; *P*, maxillary palpi; *Q*, maxillary lobarium; *R*, labial palpi; *S*, maxillary stipites; *T*, tentorial pons; *V*, fore arms of the tentorium broken on purpose; *X*, hypostomal laminae; *Y*, diverging sutures; *Z*, frontal apodema.) 5, idem, palate. 6, idem, mandible. 7, idem, distal portion of the labium with the labial palpi.

PLATE 6

1, 2, *Cionus scrophulariae* L., larva, head, dorsal and ventral views. Gnathites are not drawn. (*A*, antennae; *C*, clypeus; *D*, concavity for the ventral articulation of the mandibles; *E*, epistomal apodeme; *L*, labrum; *M*, metopic suture; *O*, ocelli; *P*, palate; *T*, tentorial pons; *X*, hypostomal laminae; *Y*, diverging sutures; *Z*, frontal apodeme.) 3, 4, *C. olens* F., larva, head, dorsal and ventral views. Gnathites are not drawn. (The same lettering.) 5, 6, *Rhynchaemus alii* L., larva, head, dorsal and ventral views. Gnathites are not drawn. (*A*, antennae; *B*, hypostomal laminae; *O*, ocelli; *R*, diverging sutures.) 7, idem,

anterior portion of the head capsule, more magnified (the same lettering). 8, idem, a maxilla and portion of the labium.

PLATE 7

Macrosiagon ferrugineum flabellatum F. 1, adult. 2, larva of the 1st phase, jejune, ventral view. 3, idem, head and portion of the prothorax, ventral view (*A*, antennae; *L*, labium; *M*, mandibles; *N*, maxillary stipites; *O*, ocelli; *P*, maxillary palpi). 4, larva of the 1st phase, replete, lateral view. 5, larva of the 2d phase, ventral view. 6, idem, head, frontal view (*A*, antennae; *M*, mandibles; *S*, labrum). 7, idem, a tracheal spiracle of the 7th urite.

PLATE 8

1, 2, *Hoplocampa brevis* Klug, head, dorsal and lateral views. The gnathites are not drawn. (*A*, antennae; *B*, paraclypeofrontal apodeme; *CI*, clypeofrontal membrane; *D*, epistomal apodeme; *E*, invagination of the fore arms of the tentorium; *F*, frons; *G*, cranial processes for the dorsal articulation of the mandibles; *H*, glenoid pit for the ventral articulation of the mandibles; *L*, labrum; *N*, tentorial processes for the attachment of the extrinsic maxillary muscles; *O*, ocelli; *P*, hypostomal apodeme; *Q*, pleurostomal apodeme; *R*, diverging suture; *S*, metopic suture; *T*, fore arms of the tentorium; *U*, post-temporal furrow; *Y*, dorsal arms of the tentorium; *Z*, postoccipital apodeme). 3 to 5, *Caliroa limacina* Retz., larva, head, dorsal, lateral, and ventral views (the lettering as above, plus *I*, hypostoma; *J*, foramen magnum; *K*, palate; *M*, hypostomal process for the attachment of the muscles of the tentorium; *P*, hypostomal suture; *X*, tentorial bar). 6, idem, head, thorax and 1st four urites, lateral view (*S*, atrophic tracheal spiracles of the metathorax; *Z*, prothoracic glandular prominences). 7, *Janus compressus* F., larva, head. Mandibles are not drawn. (*A*, antennae; *B*, fore arms of the tentorium; *C*, clypeus; *D*, diverging sutures; *E*, epistomal apodeme; *FO*, foramen magnum.) 8, idem, labrum. 9, 10, idem, left and right mandible. 11, *Pelmatopus mentiens* Thoms., larva, head, thorax, and 1st two urites, lateral view. 12, *Phyllotoma aceris* McLachl., distal portion of the left maxilla and prelabium, dorsal view (*G*, galea; *LI*, lacinia; *S*, maxillary stipes).

PLATE 9

1 to 3, *Pelmatopus mentiens* Thoms., larva, head, dorsal, lateral, and ventral views. Mandibles are not drawn (the same lettering, plus *V*, maxillary cardines; *Z*, cervical sclerites). 4, *Phyllotoma microcephala* Kl., larva, head, dorsal view (the same lettering). 5, idem, mandible. 6, idem, mandible of the last larval stage. 7, *Fenusa ulmi* Sund., larva, dorsal view of the head. Mandibles are not drawn. (The same lettering.) 8, idem, portions of the prothorax and mesothorax, ventral view (*A*, juxtapedal ambulacral areae; *B*, sternal areola with sclerotized integument; *Z*, cervical sclerite). 9, 10, *Fenella nigrita* Westw., larva, head, dorsal and ventral views (the same lettering, plus *V*, occipital process). 11, *Phyllotoma aceris* McLachl., larva, lateral view (the same lettering). 12, idem, head, lateral view. 13, idem, portion of the head capsule with an ocellus (*O*) and antenna (*A*). 14, idem, posterior portion of the head and

prothorax, ventral view (*A*, juxtapedal ambulacral areae; *C*, maxillary cardo; *P*, postlabium; *Q*, hypostomal apodome; *S*, maxillary stipes; *Z*, cervical sclerite).

PLATE 10

1, *Eumenes unguiculus* Vill., full-grown larva. 2, *Polistes foederatus* Kohl, full-grown larva (1, trophothylax). 3, *Dolichovespula norvegica* F., full-grown larva (2, tropholopade). 4, *Polistes foederatus* Kohl, larva, frontal view of the head. 5, idem, mandible. 6, *Eumenes unguiculus* Vill., larva, prelabium and a maxilla. 7, idem, maxillary palpus and galea more magnified. 8, *Polistes foederatus* Kohl, larva, a maxilla and the labium. 9, *Dolichovespula norvegica* F., larva, a maxilla and the labium. 10, idem, external organ of the labium at the bottom of which the duct of the labial glands opens. 11, *Apis mellifica* L. *ligustica* Spin., larva, left side of the labrum and left mandible. 12, idem, prelabium and a maxilla.

PLATE 11

1, *Ficus carica* L., portion of the distal end of a receptacle in correspondence with the ostiole, seen in longitudinal section in order to show the peculiar arrangement of the ostiolar scales (phyllomes). (*O*, horizontal scales; *R*, receptacle cavity; *T*, outer scales covering the ostiolar opening; *V*, inner scales folded.) 2, *F. carica* L., female galligenous flower (*G*, ovary transformed into a gall; *P*, peduncle; *Q*, perigonial lacinae; *S*, style; *T*, stigma). 3, male of *Blastophaga psenes* L. fertilizing a female (the latter still within the gall) after having introduced into the gall a portion of his abdomen. 4, *Ficus gibbosa* Blum. (Java), collective fruit with three exit holes of adults of *Neosycophila omeomorfa* Grnd. 5, 6, portions of the walls of the same collective fruit. 7, 8, *Ficus gibbosa* Blum., portions of the section of other collective fruits in correspondence with gall (*G*) of *Neosycophila omeomorpha* Grnd. 9, 10, *Ficus gibbosa* Blum., portions of the section of a collective fruit showing the gallery bored by the hymenopteran within the peduncle (*P*) of the gall-flower, before reaching the receptacle wall (*E*). (The same lettering.)

PLATE 12

1, *Blastophaga psenes* L., frontal view of the head of a female (*A*, scape of the antennae, the other portions of them are not drawn; *C*, medial longitudinal carina; *I*, region with membranous integument; *M*, groove with which the mandibles articulate; *Oc*, ocelli; *Z*, a more sclerotized region of the integument). 2, *Ceratosolen bisulcatus* Mayr, frontal view of the head of a female. 3, *Tetrapus ecuadoranus* Grnd., female, head, frontal view. 4, *Allotriozoon prodigiosum* Grnd., frontal view of the head of a female (*T*, toruli of antennae). 5, *Agaon paradoxum* (Dalm.) Grnd., frontal view of the head of a female (*T*, toruli of antennae). 6, *Pleistodontes regalis* Grnd., frontal view of the head of a female. 7, idem, a portion of a female fore leg. 8, *Seres armipes* Watrst., a portion of a female fore leg showing the tibial armor. 9, *Ceratosolen silvestrianus* Grnd., hind leg of a female.

PLATE 13

1, *Blastophaga psenes* L., female, distal portion of the scape of an antenna and 2d, 3d, and 4th joints (*a*, *b*, *c*, the three portions of the 3d joint). 2, *Ceratosolen elisabethae* Grnd., antenna of a female. 3, *C. mugatorius* Grnd., female, distal portion of the scape of an antenna; 2d, 3d, 4th, 5th joints and proximal portion of the 6th joint, showing the backward, toothlike bristles of the 2d antennomere. 4, *Eupristina koningsbergeri* Grnd., female, antenna. 5, *Tetrapus mexicanus* Grnd., antenna of a female. 6, *Agaon paradoxum* (Dalm.) Grnd., antenna of a female. 8, 9, more magnified details of the same. 10, *Tetrapus americanus* Mayr, female, a proximal portion of a fore wing. 11, *T. mexicanus* Grnd., female, distal end of a hind tibia, tarsus, pretarsus of a fore leg. 12, *Julianella baschierii* Grnd., female, distal end of a hind tibia. 13, *Pleistodontes regalis* Grnd., female, a hind leg.

PLATE 14

1, *Ceratosolen acutatus* Mayr, female, mandible. 2, *C. silvestrianus* Grnd., female, mandible. 3, *C. elisabethae* Grnd., female, mandible. 4, *Eupristina koningsbergeri* Grnd., female, mandible. 5, *Tetrapus ecuadoranus* Grnd., female, mandible. 6, *T. mexicanus* Grnd., female, mandible. 7, *Pleistodontes froggatti* Mayr, female, mandible. 8, *Ceratosolen acutatus* Mayr, female, maxillolabial complex. 9, *C. silvestrianus* Grnd., female, maxillolabial complex. 10, *Allotriozoon prodigiosum* Grnd., female, maxillolabial complex. 11, *Tetrapus costaricanus* Grnd., female, maxillolabial complex. 12, *Pleistodontes regalis* Grnd., female, maxillolabial complex. 13, *Ceratosolen silvestrianus* Grnd., female, fore leg. 14, idem, middle leg.

PLATE 15

1, *Blastophaga psenes* L., male with the last urites extroflexed (*A*, antennae; *a*, coxae of the legs; *C*, head; *E*, propleurites; *F*, femurs of the legs; *M*, mesothorax; *m*, membranous collar; *N*, metapleurites; *O*, eyes; *P*, pronotum; *p*, penis; *Q*, mandibles; *s*, tracheal spiracles; *t*, trochanters of the legs). 2, idem, abdomen with the 9th urite closed, the copulatory organ and the membranous collar invaginated. 3, idem, head, thorax, and a portion of the legs, ventral view (*a*, coxae of the legs; *b*, condyles for the ventral articulation of the mandibles; *c*, maxillolabial complex; *D*, folded sides of the pronotum; *E*, propleurites; *F*, femurs of the middle legs; *g*, distal cavities of the fore coxae; *H*, mesosternum; *J*, jugular processes of the propleurites; *o*, connecting passage between the propodeal and gastral cavity; *S*, prosternum; *t*, trochanters of the middle legs). 4, *B. ghigii* Grnd., male, head. 5, *B. intermedia* Grnd., male, head. 6, *B. longicornis* Grnd., male, head. 7, *B. giacomini* Grnd., male, head. 8, *B. (Waterstoniella) jacobsoni* Grnd., male, head seen in dorsal view. 9, idem, ventral view (*B*, residue of the mouth opening; *O*, foramen magnum). 10, idem, residue of the mouth opening more magnified. 11, *Ceratosolen bisulcatus* Mayr, male, head (the right antenna is not drawn).

PLATE 16

1, *Blastophaga astoma* Grnd., male, head. 2, *B. psenes* L., male, 9th urotergite, membranous collar, copulatory organ quite extroflexed (*C*, membranous collar;

M, cuticular reinforcement; *N*, proximal processes of the penis; *P*, penis; *Q*, gonopore). 3, *B. (Waterstoniella) jacobsoni* Grnd., male, thorax and propodeum. 4, *Eupristina koningsbergeri* Grnd., male, thorax and propodeum. 5, *E. aurivilli* Mayr, male, thorax and propodeum. 6, *Blastophaga giacomini* Grnd., male, thorax and propodeum. 7, *B. ghigii* Grnd., male, sternopleural, promesothoracic and metathoracic regions and portion of the legs (*C*, rudiments of the mesothoracic legs; *S'*, prosternum; *S''*, mesosternum). 8, *B. boldinghi* Grnd., male, thorax and abdomen, dorsal view. 9, idem, thorax and propodeum, ventral view. 10, idem, more magnified ventral view of the thorax (*d*, pronotum; *E*, propleurites; *e*, mesonotum; *f*, metanotum fused with metapleurites; *k*, anterior portion of the pronotum movable and articulated with the portion that is behind; *S*, tracheal spiracles; *S'*, prosternum fused with the propleurites; *S''*, mesosternum; *S'''*, metasternum; *x*, processes of articulation of the anterior part of the pronotum).

PLATE 17

1, *Blastophaga giacomini* Grnd., male, antenna. 2, *B. (Waterstoniella) jacobsoni* Grnd., male, antenna. 3, *Eupristina aurivilli* Mayr, male, antenna. 4, *Ceratosten striatus* Mayr, male, antenna. 5, *Blastophaga psenes* L., mandible, dorsal view. 6, idem, ventral view (*e, d, f*, teeth of the distal portion; *Z*, condyle for the ventral articulation). 7, *B. psenes* L., male, maxillolabial complex (*W*, maxillae of the first pair; *X*, labium; *x*, portion of the labium including the subatrophied labial palpi). 8, *B. nipponica* Grnd., male, maxillolabial complex. 9, *B. ghigii* Grnd., male, rudiment of the maxillolabial complex. 10, *Eupristina emeryi* Grnd., rudiment of the maxillolabial complex. 11, *Blastophaga intermedia* Grnd., female, fore leg (coxa excluded). 12, *B. giacomini* Grnd., male, fore leg (coxa excluded). 13, 14, *Tetrapus mexicanus* Grnd., male, distal portion of the femur, tibia, and tarsus of the fore leg, seen from the outer and inner surfaces. 15, *Blastophaga longicornis* Grnd., male, middle leg. 16 to 18, *B. giacomini* Grnd., male, middle legs in various degrees of involution. 19, *B. gestroi* Grnd., male, middle leg. 20, *Tetrapus mexicanus* Grnd., middle leg reduced to a biarticulate knot. 21, *Blastophaga giacomini* Grnd., male, hind leg (coxa excluded). 22, *Tetrapus costaricanus* Grnd., male, distal end of the tibia and metatarsus.

PLATE 18

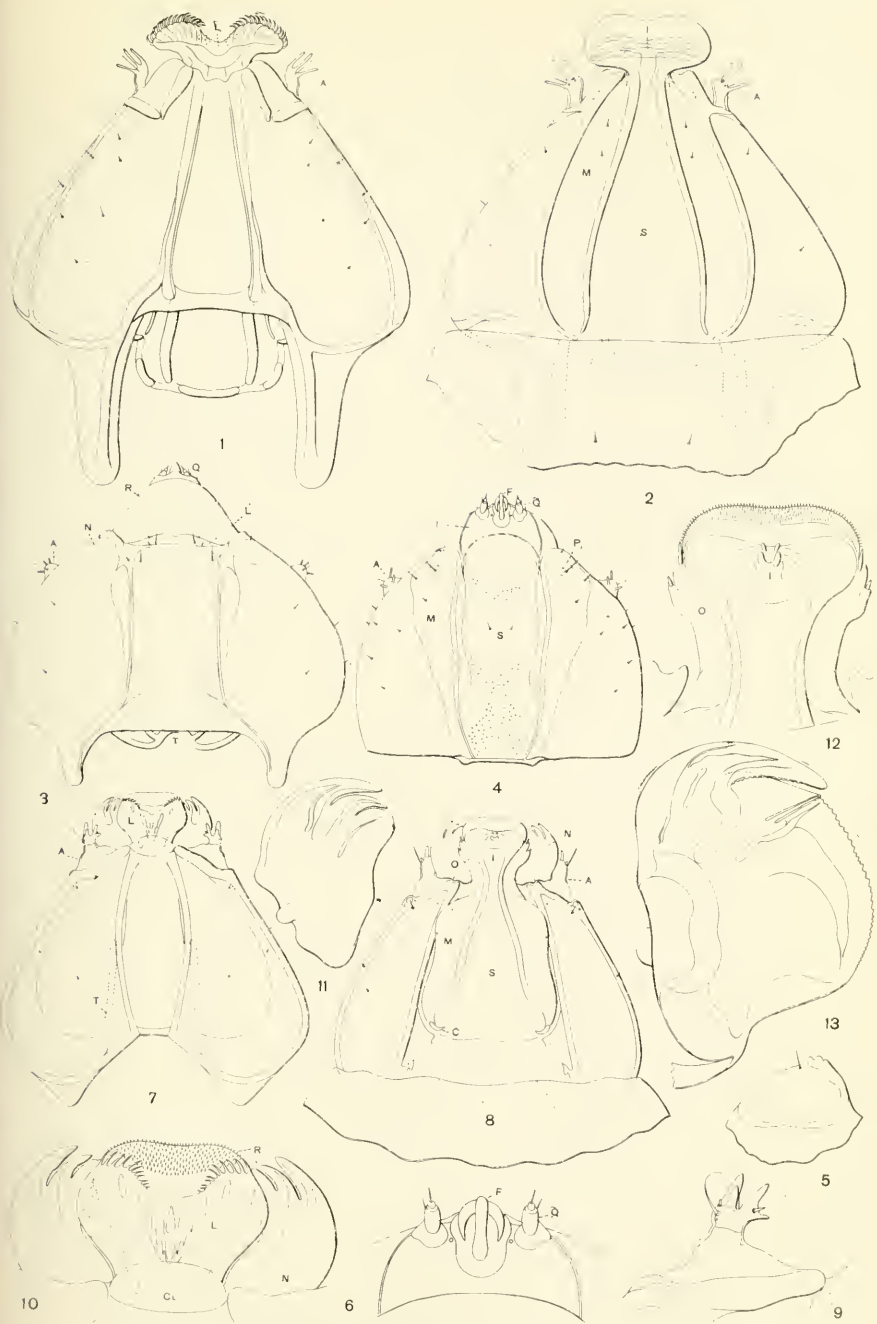
1, *Philocaenus barbatus* Grnd., female, ventral view of the head (the mandibles (*M*) have been only outlined). 2, 3, idem, mandibles, dorsal and ventral views. 4, *Lipothymus sumatranus* Grnd., female, hind leg. 5, *Sycoccus thaumastocnema* Waterst., female, fore leg (*L*, large laminar organ of the tibia covered with a series of small indentations, but only outlined) (after Waterston). 6, *Philothrypsis caricae* L., female, uroterga separated and extended (*S*, tracheal spiracles). 7, idem, eumegetic male (*A*, pronotum; *a*, fore wings; *B*, mesonotum; *b*, hind wings; *C*, metathorax; *D*, propodeum; *e*, proximal processes of the penis; *f*, hind coxae; *H*, genital armature; *p*, penis; *s*, tracheal spiracles). 8, idem, hypomegetic male (*a*, fore wings; *p*, hind wings, all rudimentary). 9 to 14, idem, wings of several males in various stages of involution (*A*, fore wing; *a*, axillary sclerite of the fore wing; *B*, scale of the fore wing; *E*, mesopleural region; *P*, hind wing; *S*, metapleural region; *s*, axillary sclerite of the hind wing).

PLATE 19

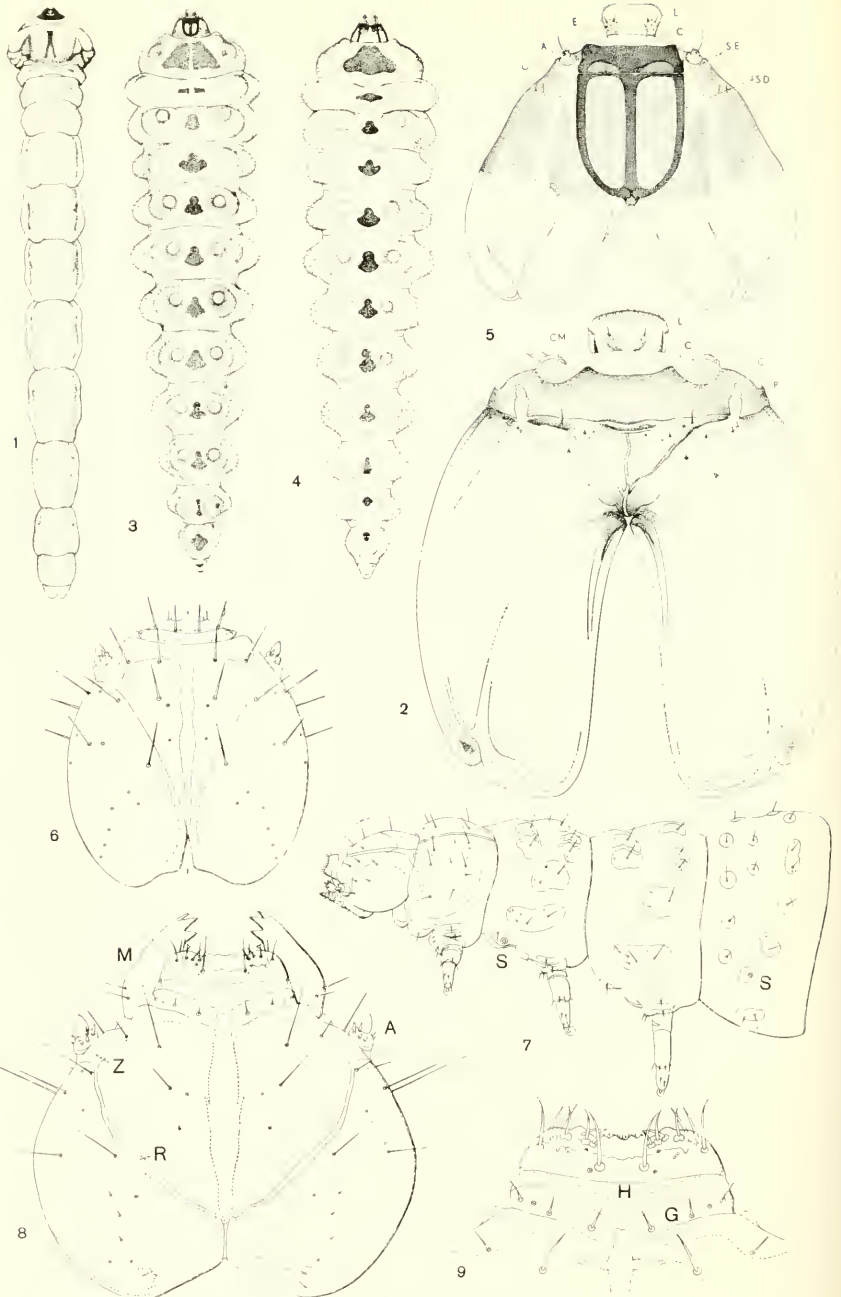
Eukoebelia Ashm., various species, males. 1, head and thorax, ventral view (*A*, antennae; *C*, *C'*, *C''*, coxae of the three pair of legs; *E*, propleurites; *L*, maxillolabial complex; *M*, mandibles; *O*, foramen magnum; *S*, *S'*, *S''*, sterna of the three thoracic segments). 2, head. 3, head, where the anterodorsal portion has been disjointed from the portion behind. 4, 5, heads. 6, 7, thoraxes and propodea. 8 to 10, fore, middle, and hind legs.

PLATE 20

1, *Hedychrum nobile* Scop., dorsal view of the female abdomen with caudal urites extroflexed. 2, idem, 2d to 4th urites, ventral view. 3, idem, 7th and 8th urites, lateral view. 4, idem, dorsal view of the male abdomen with caudal urites extroflexed. 5, idem, portions of the 3d and 4th urites, ventral view. 6, *Chrysis scutellaris* F., 5th urotergum, extended, of the female. 7, idem, paratergites and 2d to 4th urosterna. 8, *Parnopes grandior* Pall., male, abdomen with caudal urites introflexed (*C*, copulatory organ; *PT*, laterotergites; *S*, stigmata; 2 to 8, corresponding urites; 2*S* to 7*S*, corresponding urosterna; 2*T* to 8*T*, corresponding uroterga).

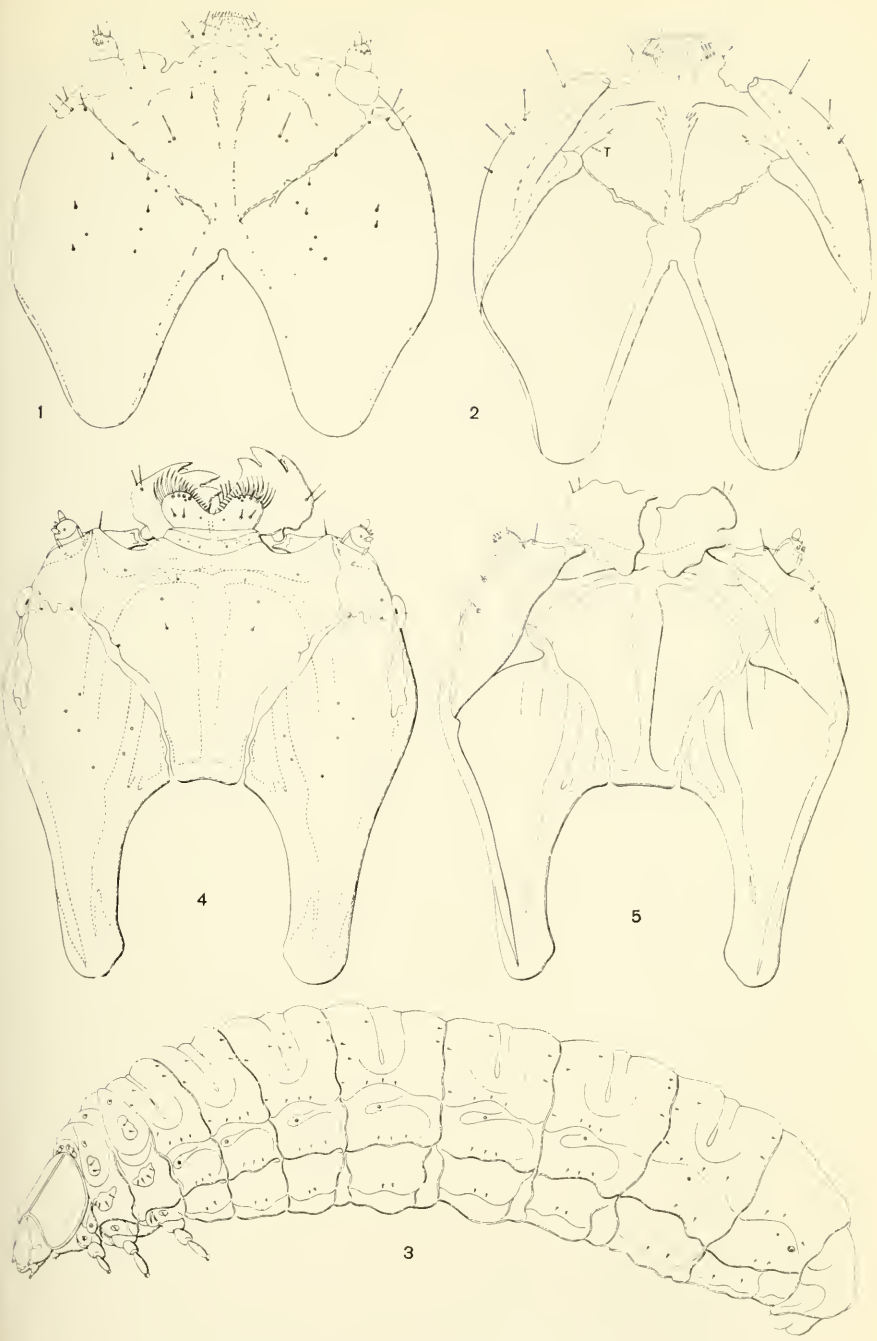


Gracilaria latifoliella, *G. stigmatella*, and *Phyllocnistis suffusella*.
 (See explanation of plates, p. 224.)

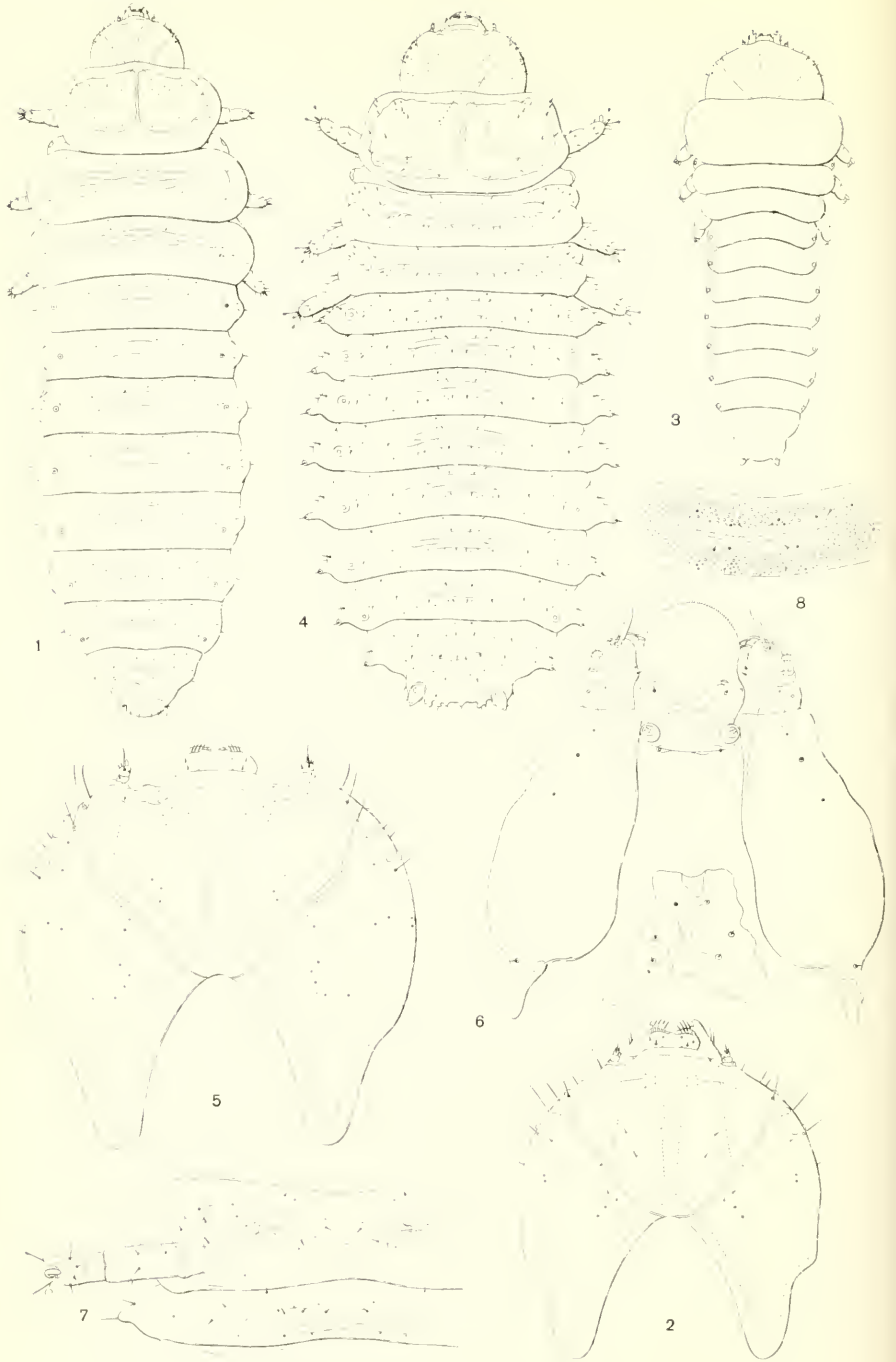


Capnodis tenabrionis, *Trachys pygmaea*, *Aphis cyparissae*, and *Phyllotreta nemorum*.

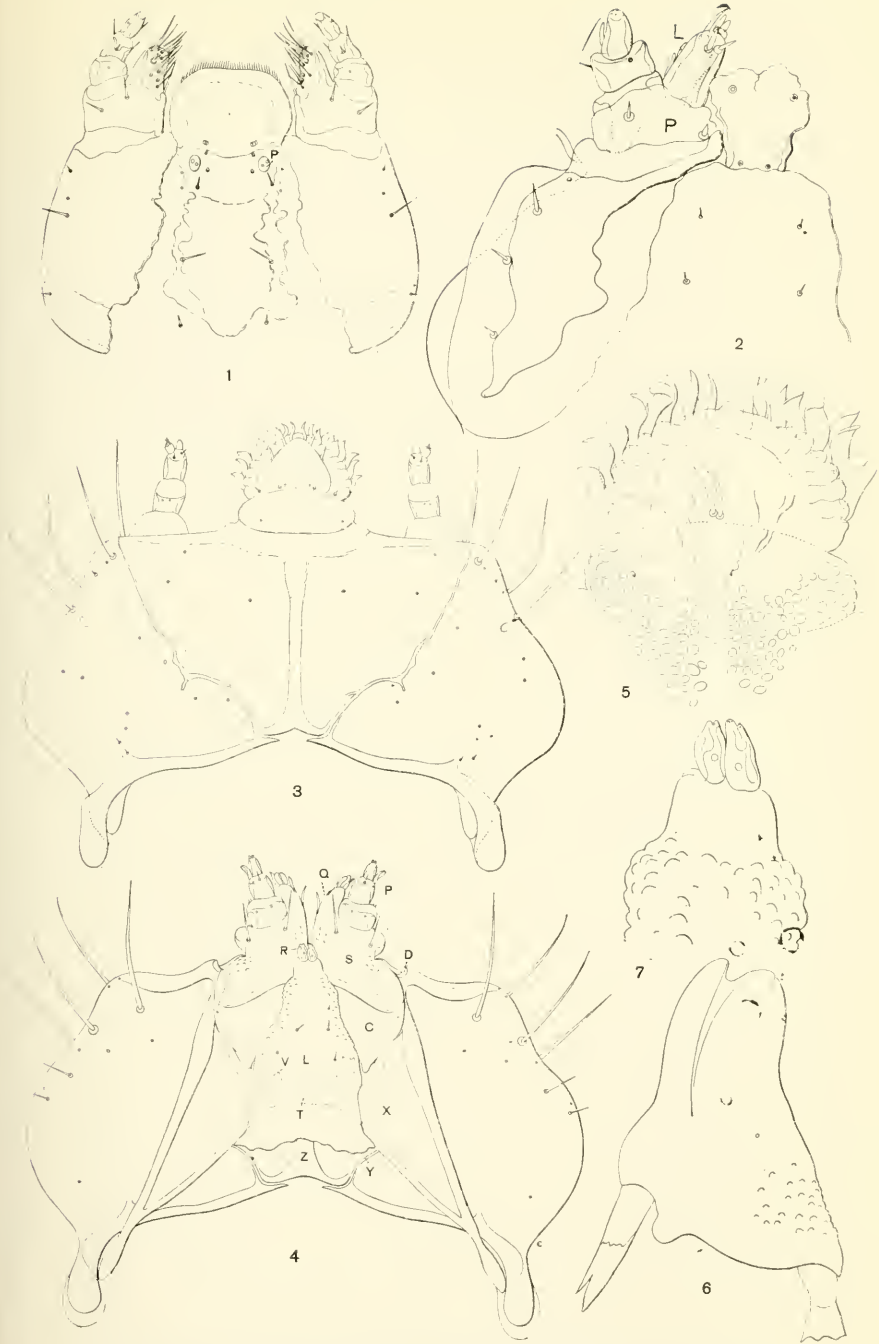
(See explanation of plates, p. 225.)



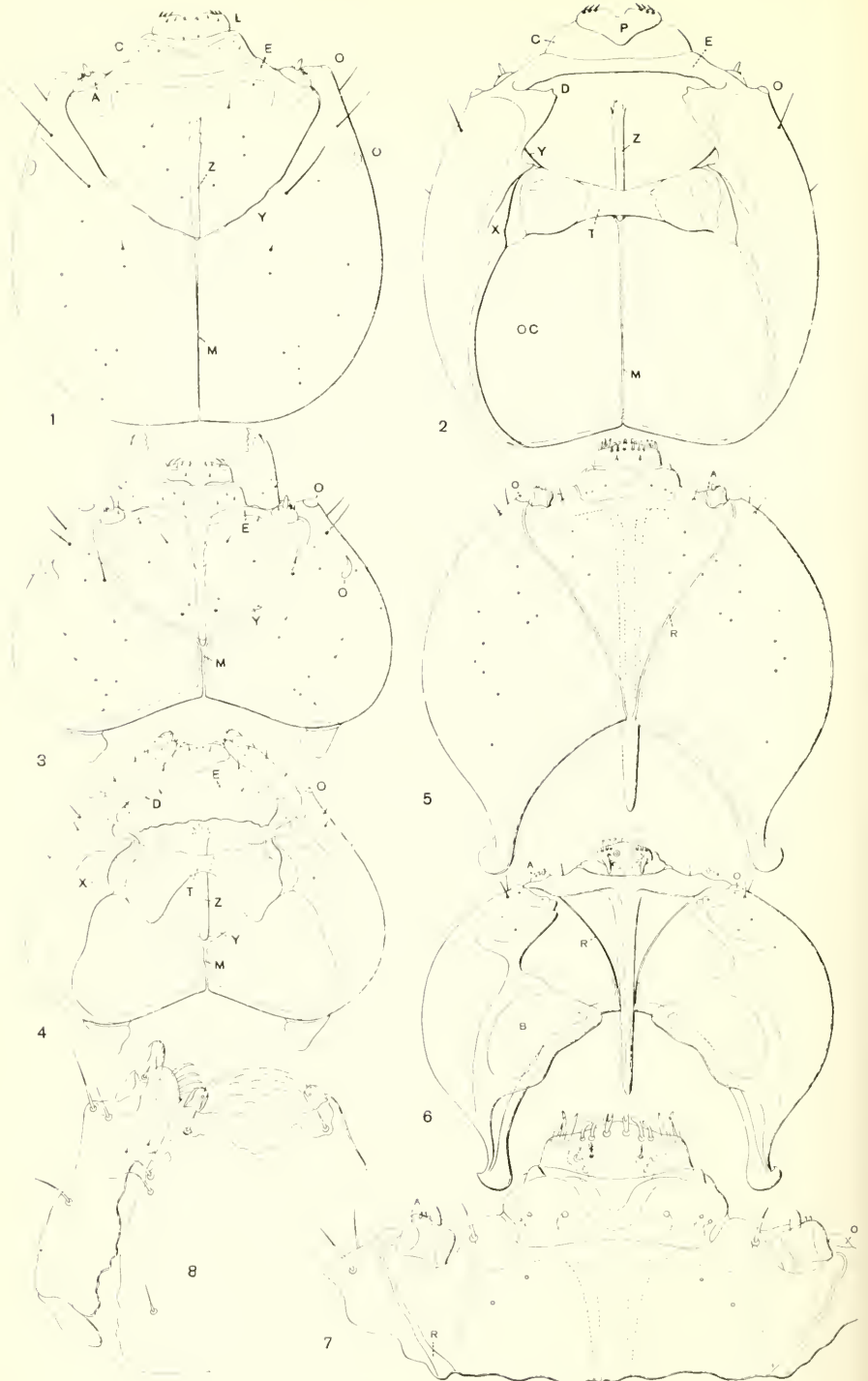
Dibolia femoralis and *Sphaeroderma rubidum*.
(See explanation of plates, p. 225.)



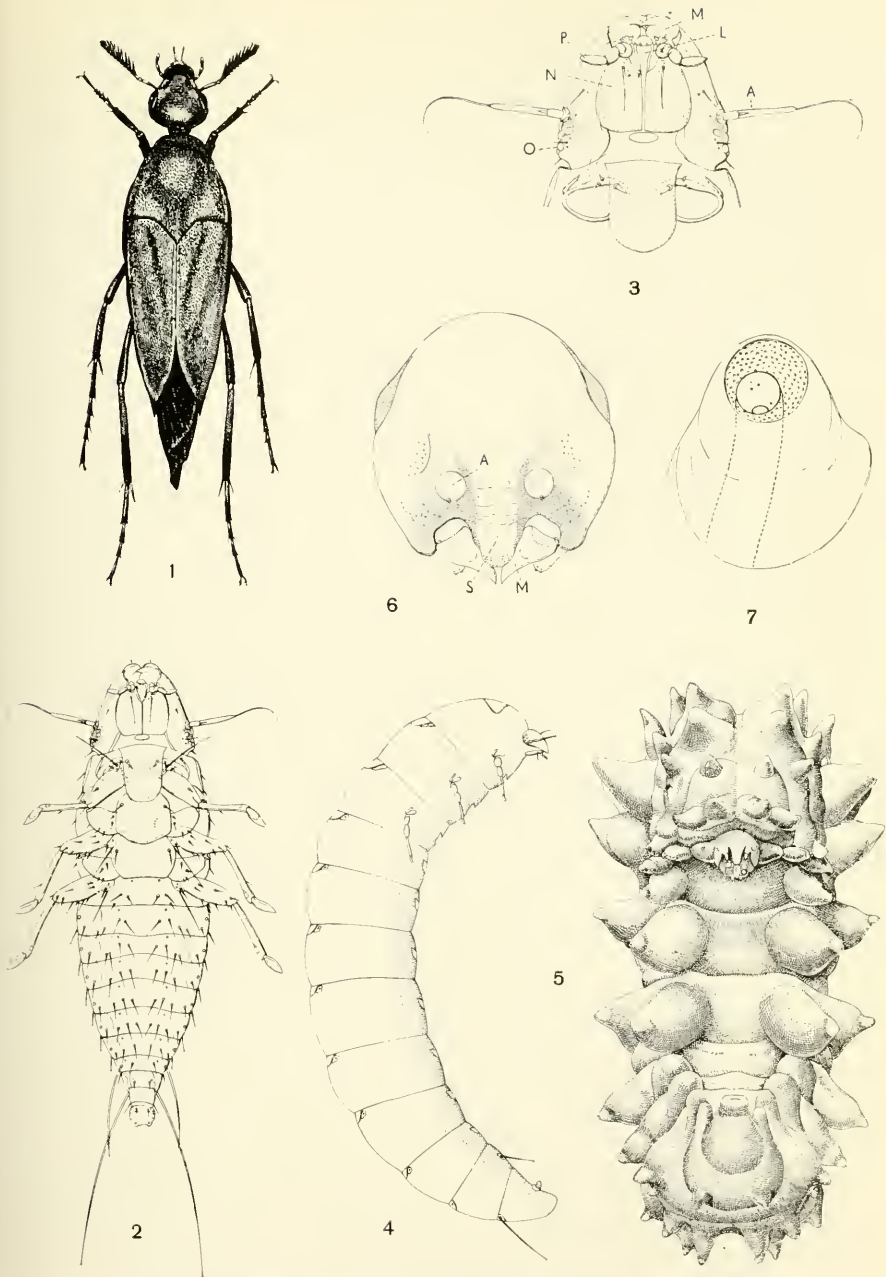
Hispella atra and *Hispa testacea*.
(See explanation of plates, p. 225.)



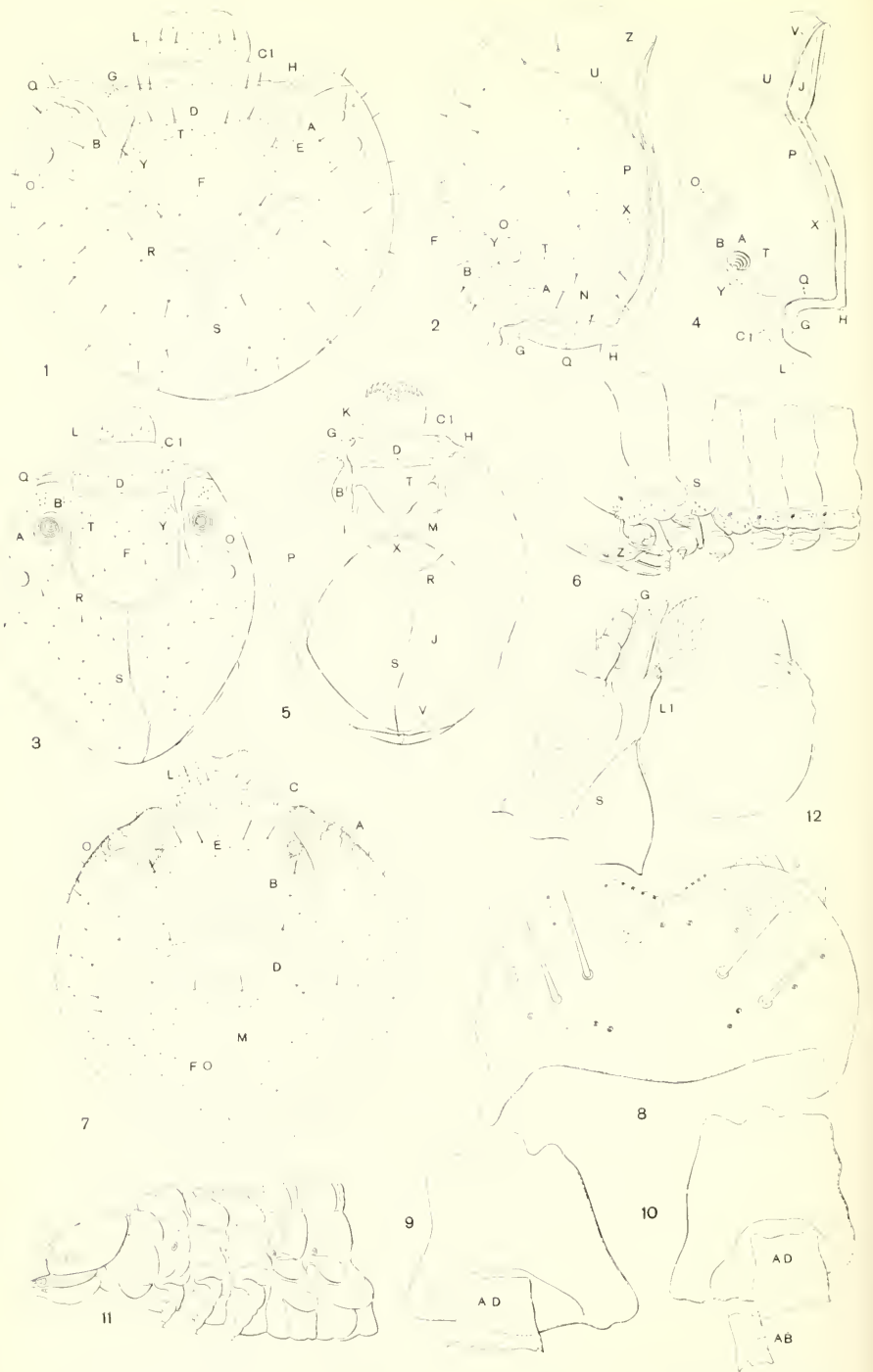
Dibolia femoralis, *Sphacroderma rubidum*, and *Zeugophora subspinoso*
(See explanation of plates, p. 225.)



Cionus scrophulariae, *C. olens*, and *Rhynchaenus alii*.
 (See explanation of plates, p. 225.)

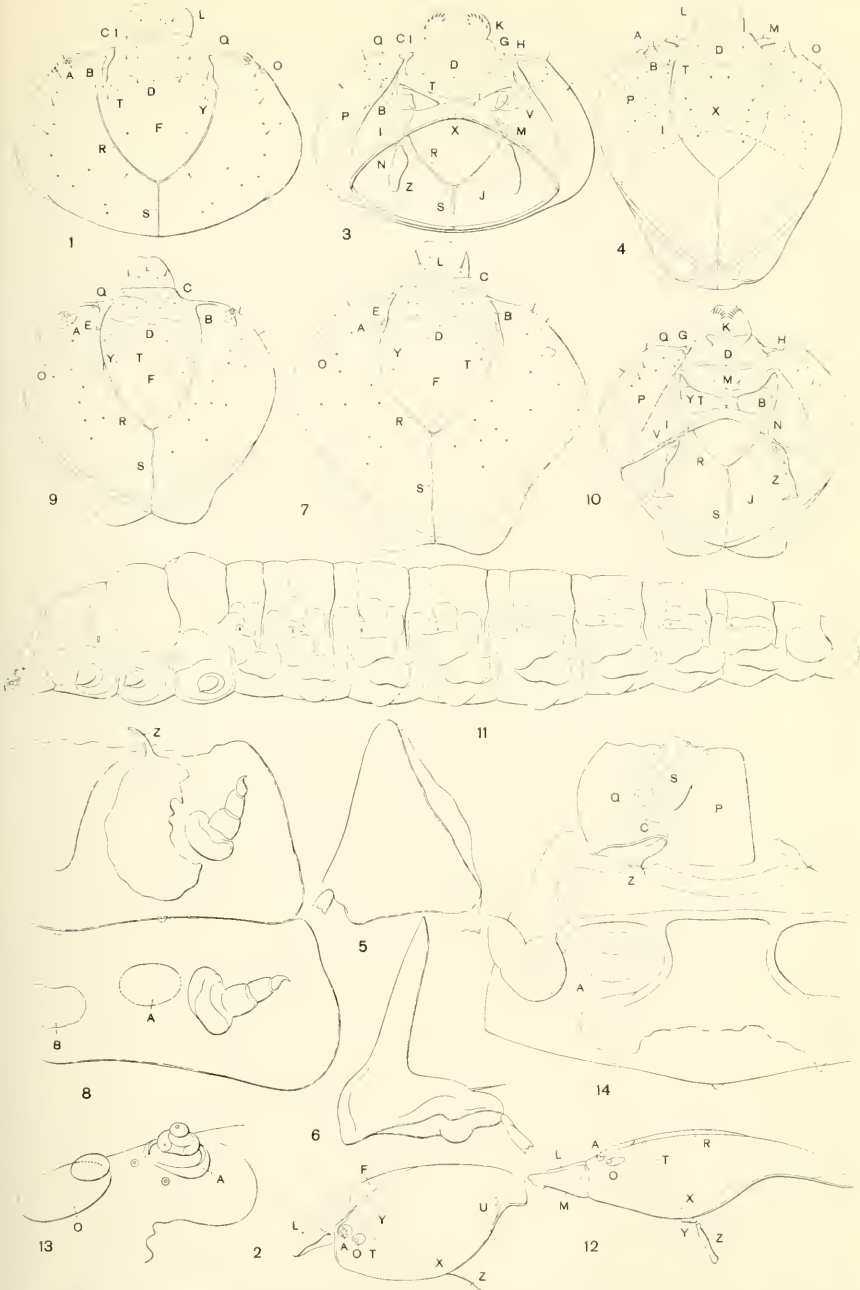


Macroisagon ferrugineum flabellatum.
(See explanation of plates, p. 226.)

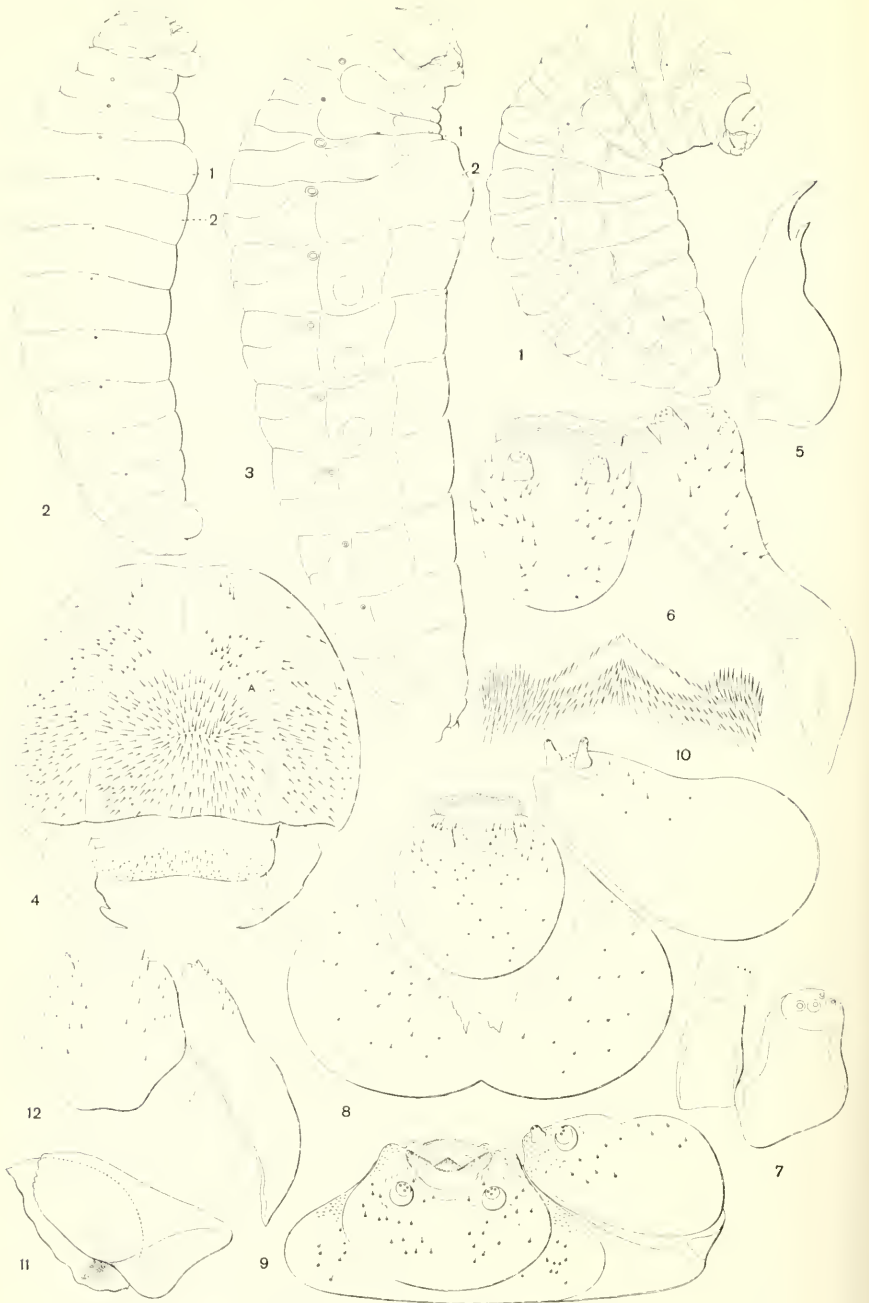


Hoplocampa brevis, *Caliroa limacina*, *Janus compressus*, *Pelmatopus mentiens*,
and *Phyllotoma aceris*.

(See explanation of plates, p. 226.)

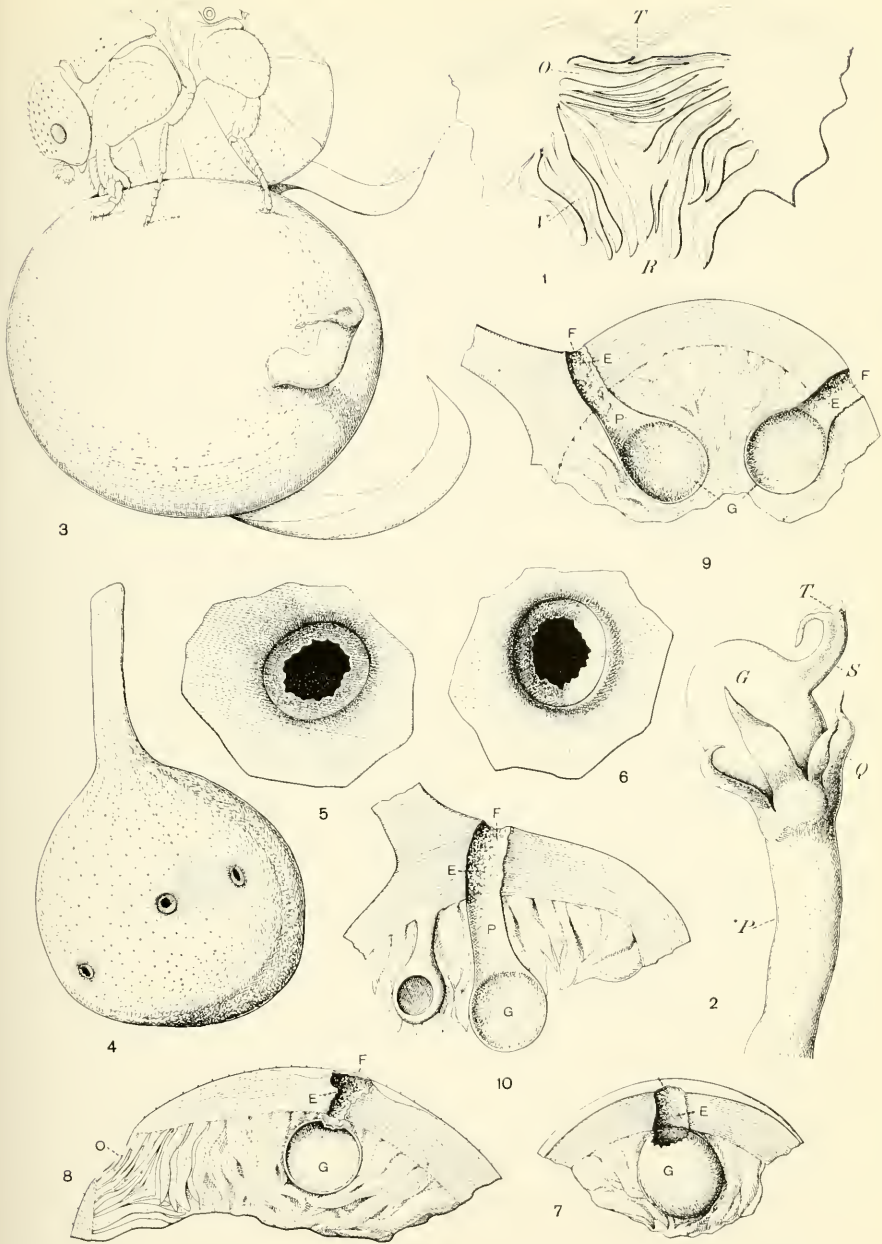


Pelmatopus mentiens, *Phyllotoma microcephala*, *Fenusa ulmi*, *Fenella nigrita*,
 and *Phyllotoma aceris*.
 (See explanation of plates, p. 226.)

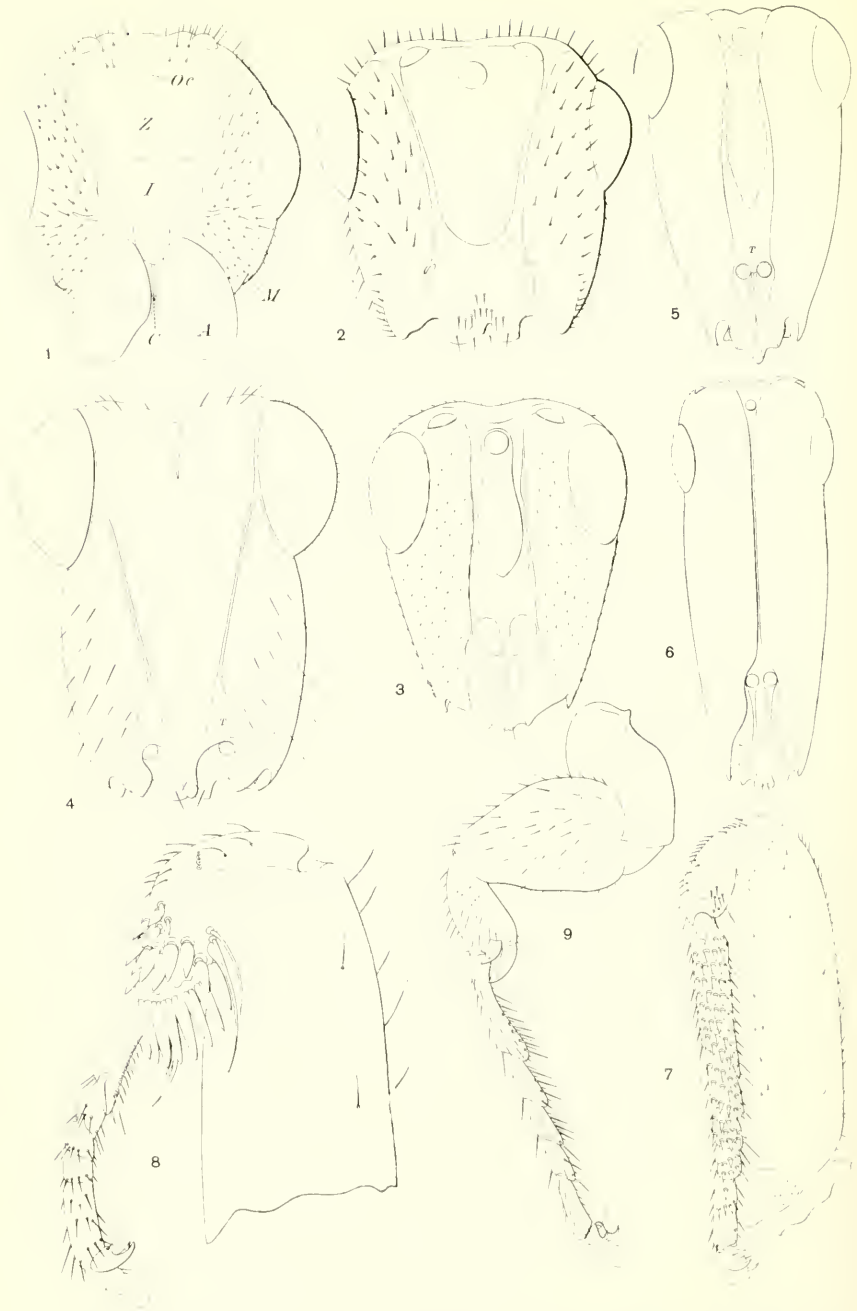


Eumenes unguiculus, *Polistes foederatus*, *Dolichovespula norvegica*, and
Apis mellifica.

(See explanation of plates, p. 227.)



Ficus carica, *F. gibbosa*, *Blastophaga psenes*, and *Neosycophila omcomorpha*.
(See explanation of plates, p. 227.)



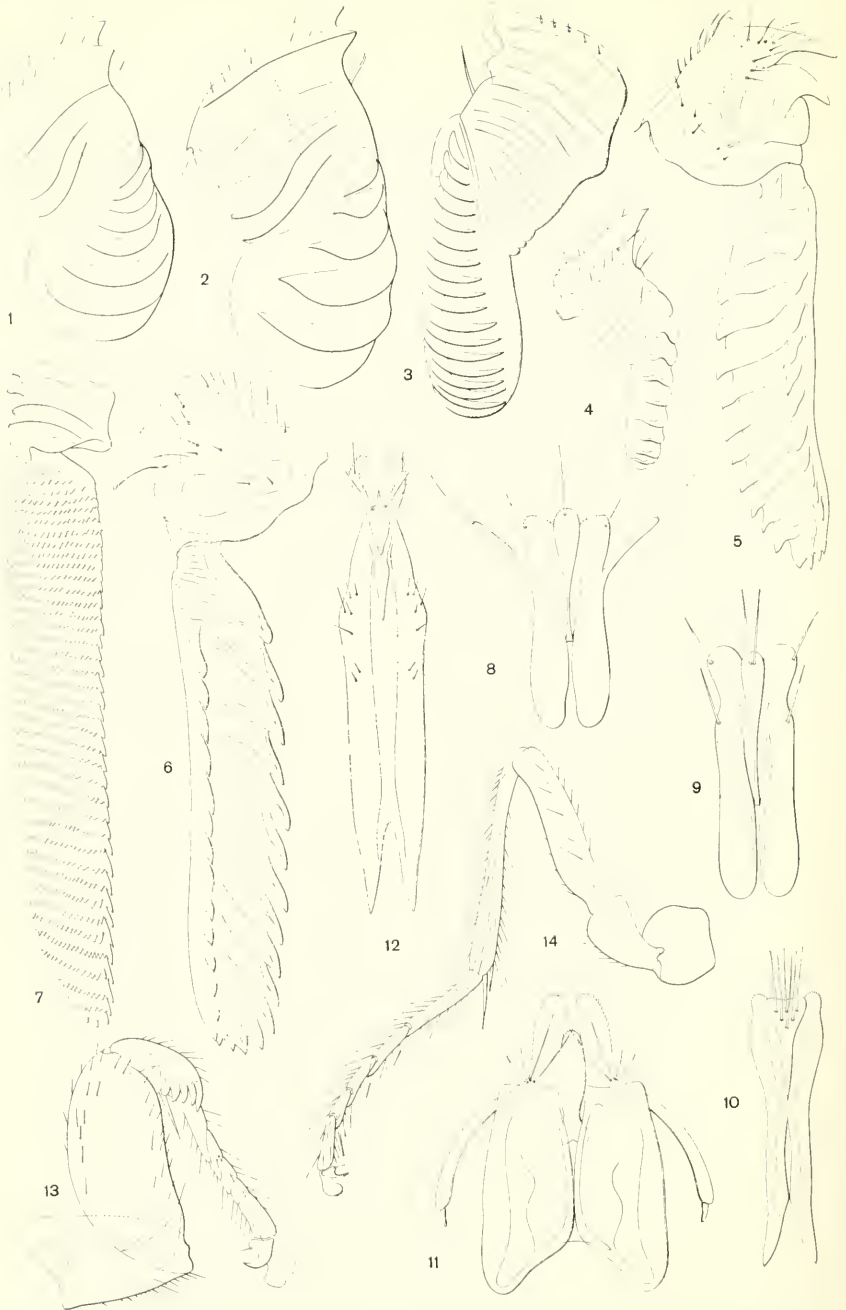
Blastophaga psenes, *Ceratosolen bisulcatus*, *C. silvestrianus*, *Tetraps ecuadoranus*, *Allotriozoon prodigiosum*, *Agaon paradoxum*, *Pleistodontes regalis*, and *Seres armipes*.

(See explanation of plates, p. 227.)



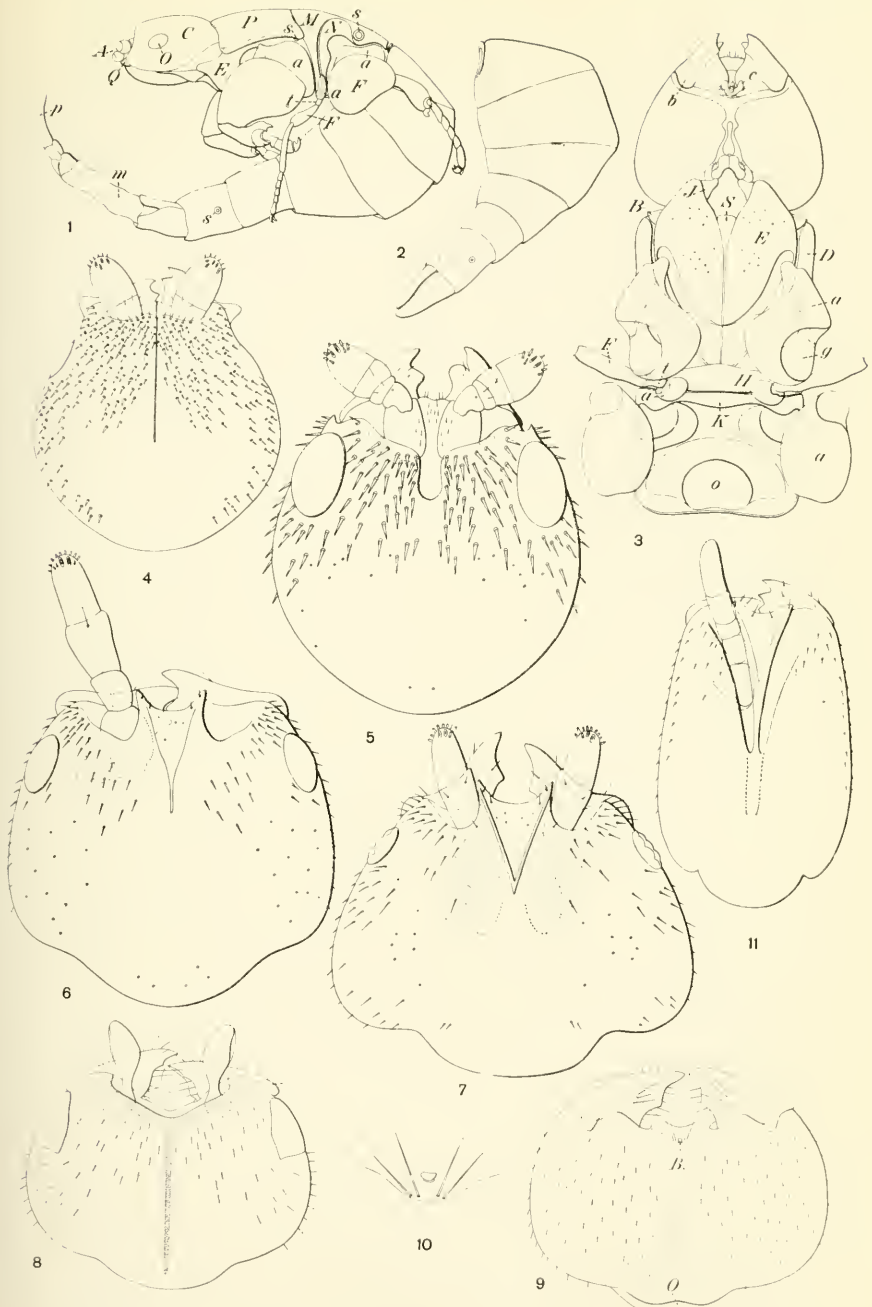
Blastophaga psenes, *Ceratosolen elisabethae*, *C. nugarorius*, *Eupristina koningsbergeri*, *Tetrapus mexicanus*, *T. americanus*, *Agaon paradoxum*, *Julianella baschierii*, and *Pleistodontes regalis*.

(See explanation of plates, p. 228.)

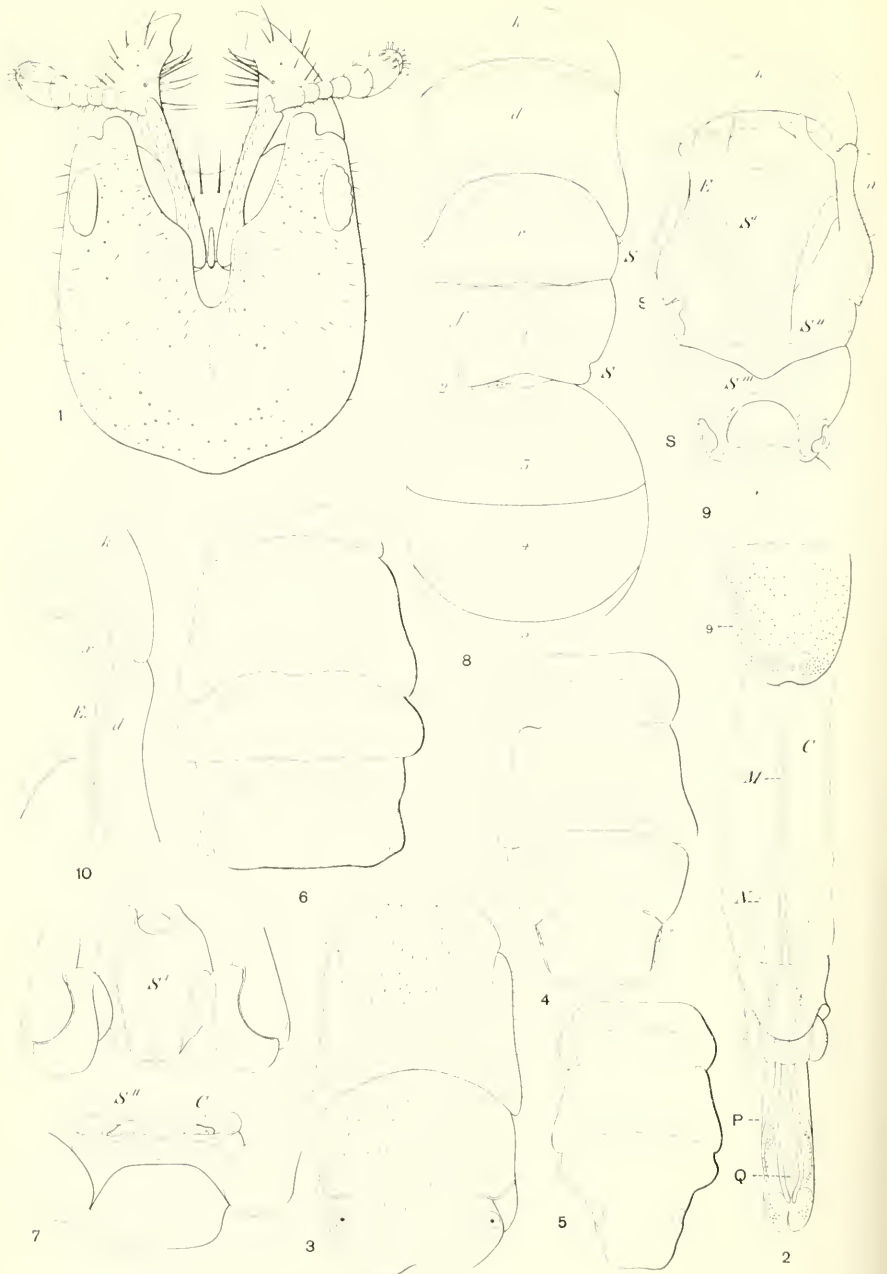


Ceratosolen acutatus, *C. silvestrianus*, *C. elisabethae*, *Eupristina koningsbergeri*,
Tetrapus ecuadoranus, *T. mexicanus*, *T. costaricanus*, *Pleistodontes froggatti*, *P.*
regalis, and *Allotriozoon prodigiosum*.

(See explanation of plates, p. 228.)

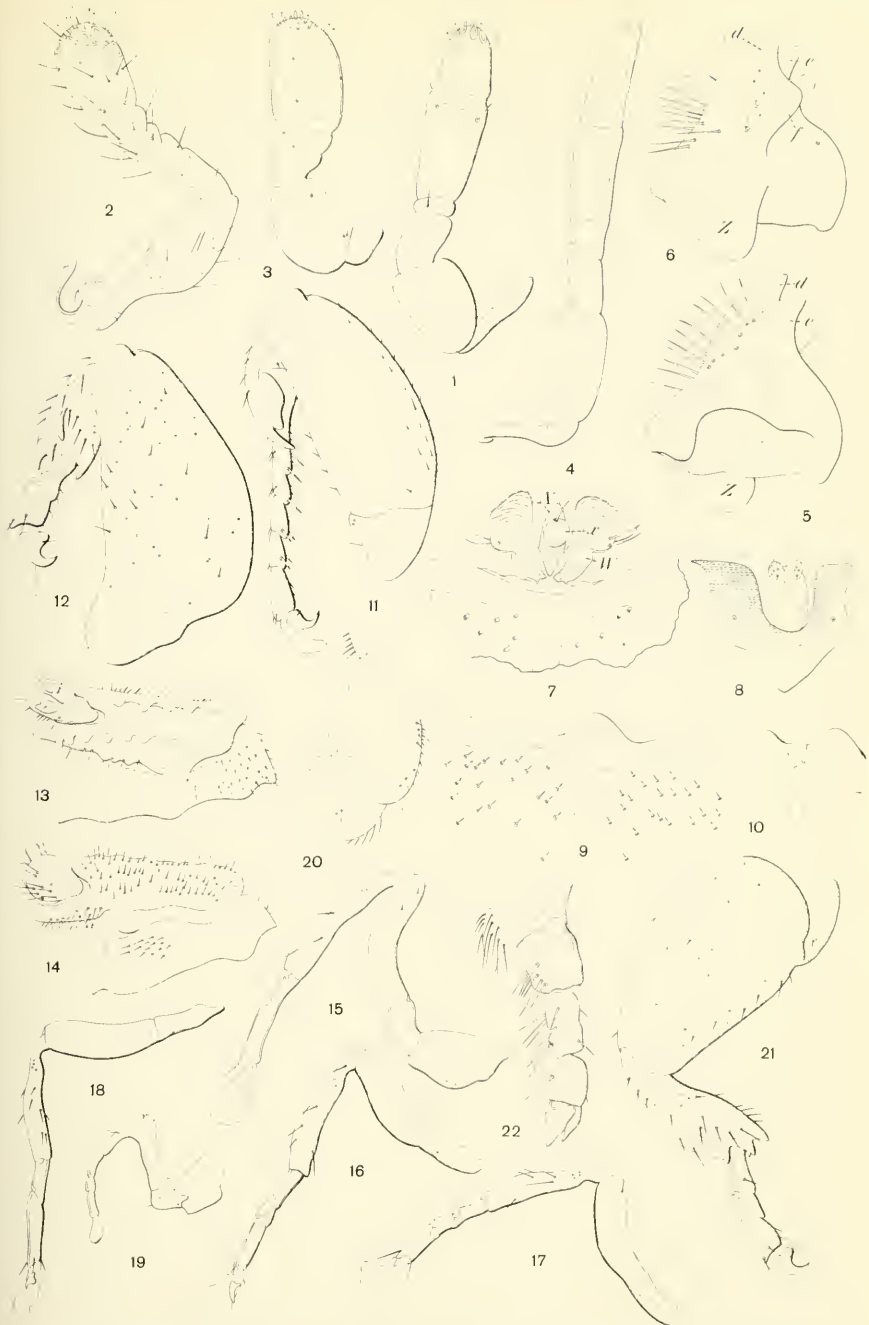


Blastophaga psencs, *B. ghigiù*, *B. intermedia*, *B. longicornis*, *B. giacomini*,
B. (Waterstoniella) jacobsoni, and *Ceratosolen bisulcatus*.
 (See explanation of plates, p. 228.)



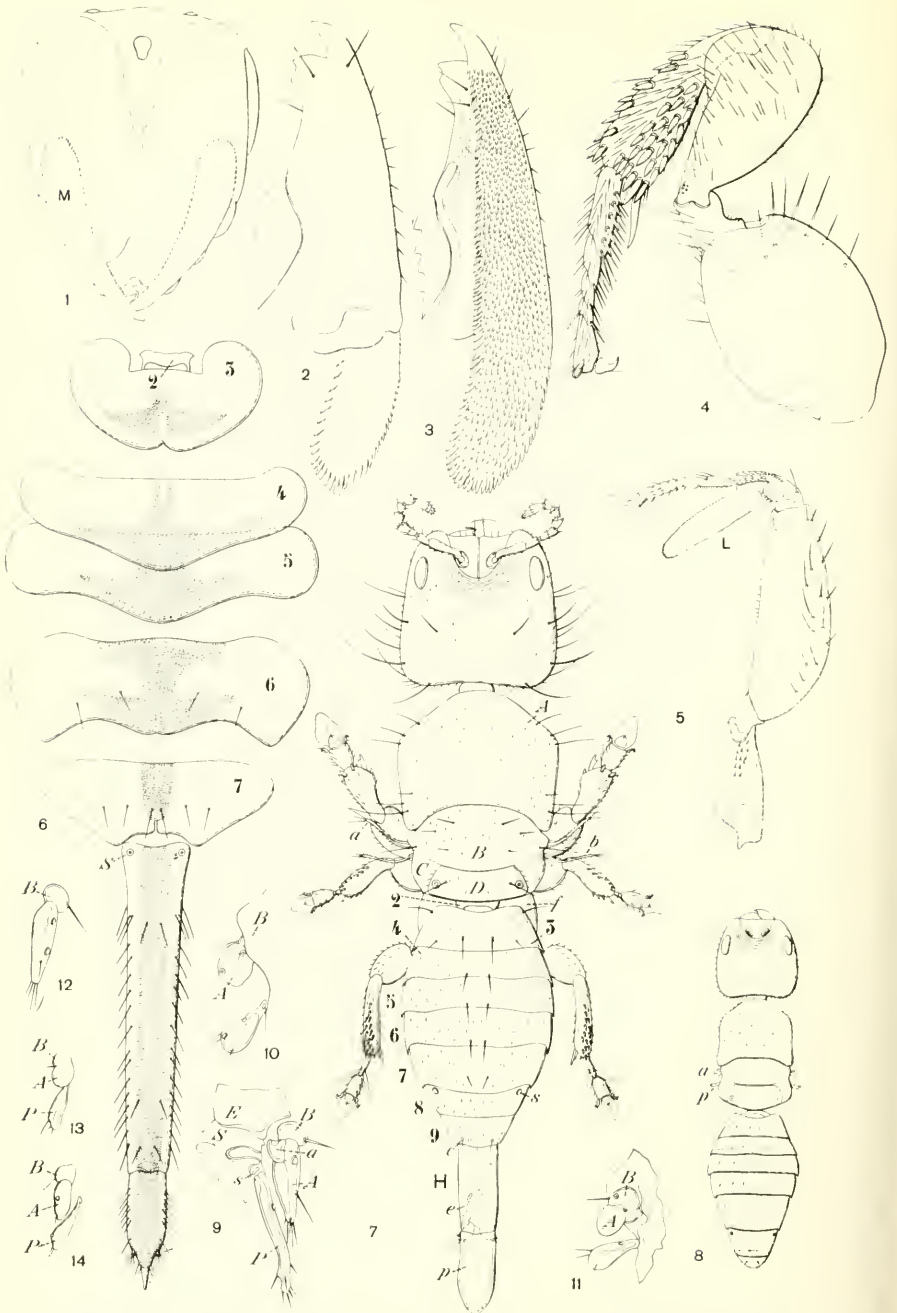
Blastophaga astoma, *B. psenes*, *B. (Waterstoniella) jacobsoni*, *B. giacomini*,
B. ghiqū, *B. boldinghi*, *Eupristina koningsbergi*, and *E. aurivilli*.

(See explanation of plates, p. 228.)



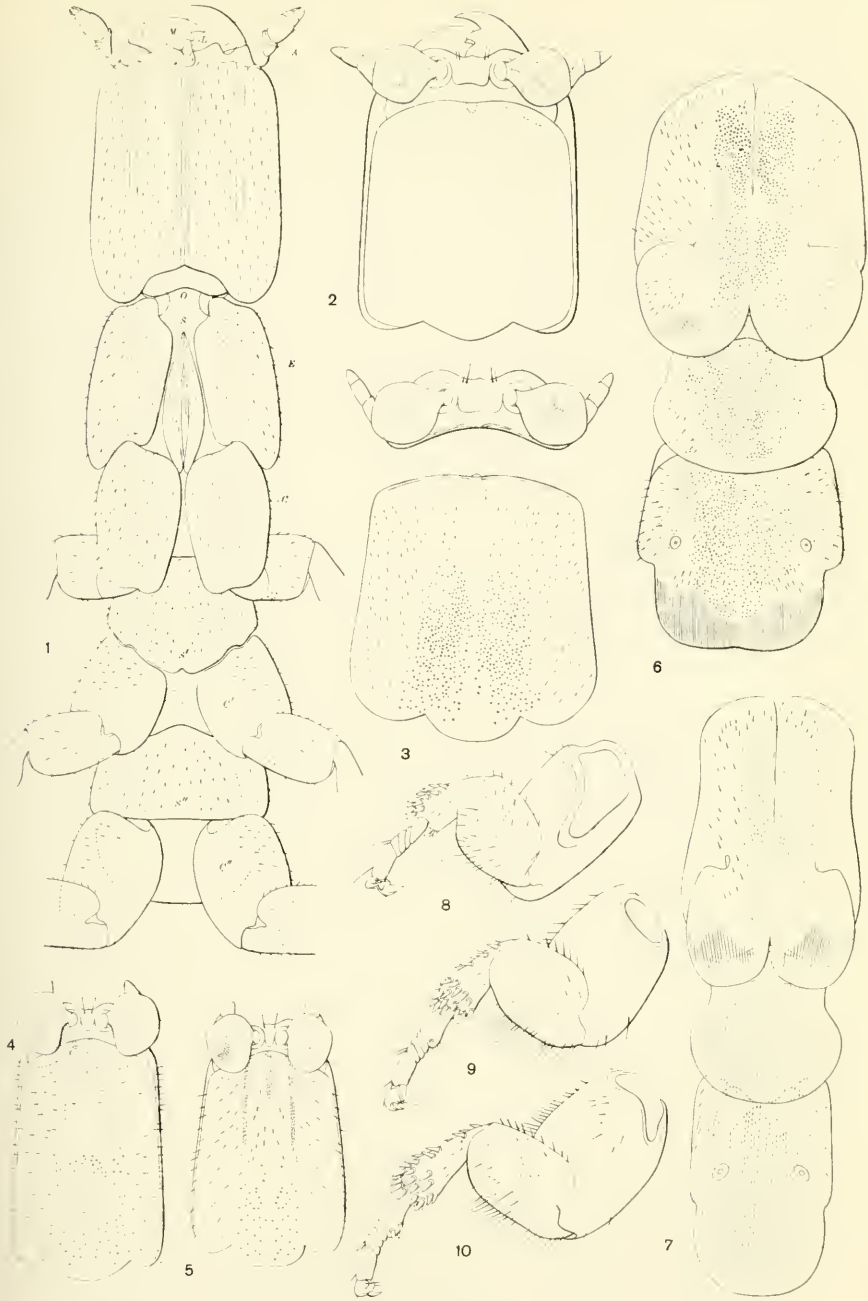
Blastophaga giacomini, *B. (Waterstoniella) jacobsoni*, *B. psenes*, *B. nipponica*, *B. ghigii*, *B. intermedia*, *B. longicornis*, *B. gestroi*, *Eupristina aurivilli*, *E. emeryi*, *Ceratosolen striatus*, *Tetrapus mexicanus*, and *T. costaricanus*.

(See explanation of plates, p. 229.)



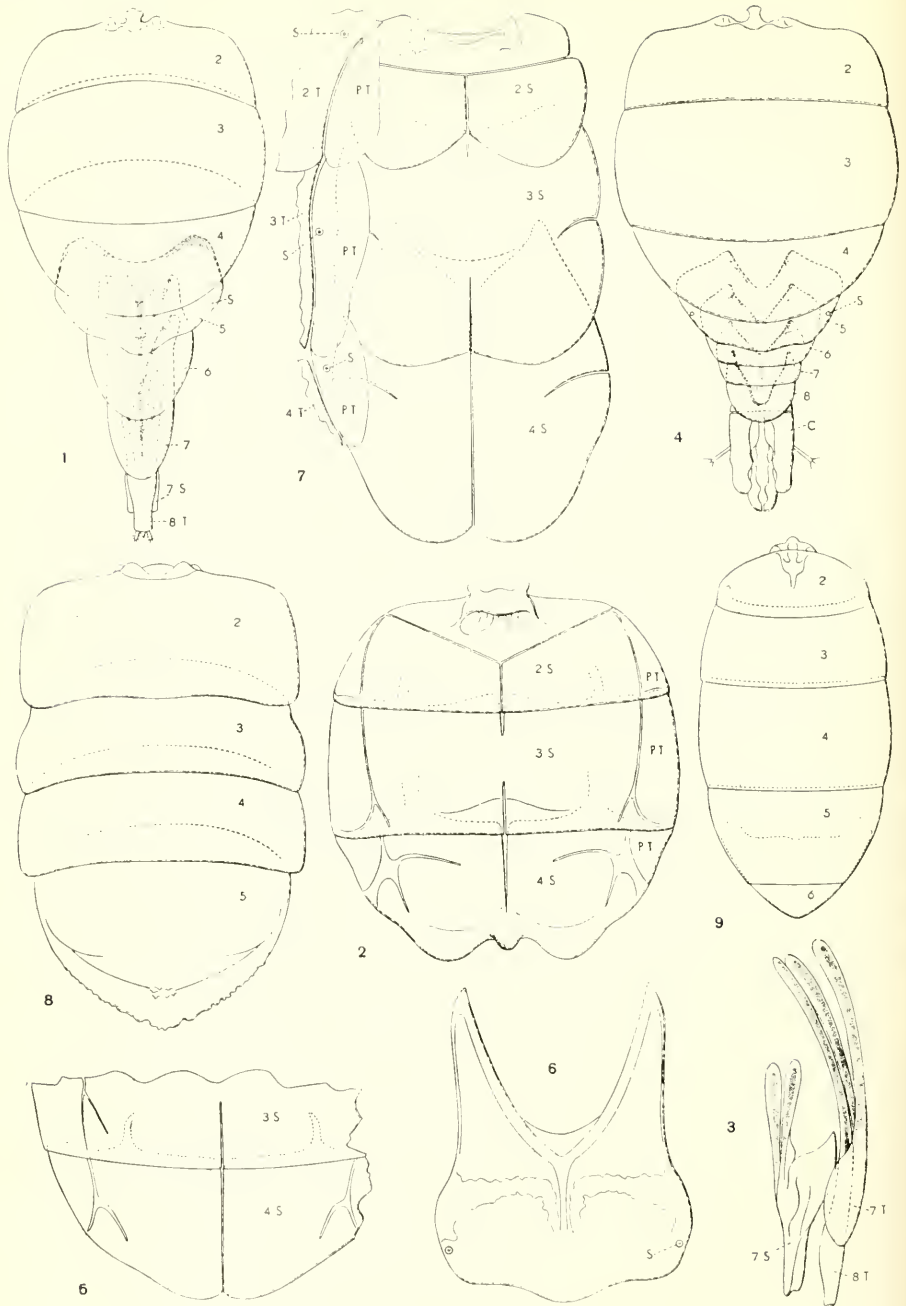
Philocaenus barbatus, *Lipothymus sumatranus*, *Sycocens thanmastocnema*, and *Philothrypesis caricae*.

(See explanation of plates, p. 229.)



Eukoebelca.

(See explanation of plates, p. 230.)



Hedychrum nobile, *Chrysis scutellaris*, and *Parnopes grandior*.
 (See explanation of plates, p. 230.)

THE SHAPING OF THE EGG STRINGS IN THE COPEPODS

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When examining the different types of egg strings in the copepods, the observer will be struck by the great variety of shape. Not only does it vary among families, but also among closely related genera—yes, even among different species of the same genus. For instance, *Brachiella ovalis* (Kr.) has small, globular egg strings. The egg strings of *Brachiella merlucii* Bassett-Smith are sausage-shaped; those of *Brachiella trigla* Claus and *Brachiella rostrata* Kroyer are long, round bands, longer than the animal itself. This variation within the same genus we find only in parasitic copepods. We have egg-shaped egg strings in the Cyclopidae, round egg balls in the Diaptomidae, and irregular egg clusters in many Harpacticidae, especially in the small forms living in the tidal zone and digging between the sand grains in the upper 1 or 2 cm. of the beach.

We find long strings with many eggs especially in parasitic copepods living in the gill chambers of fishes, or egg strings curled in a spiral held together by a mesenterial-like filament in many Lernaeidae, or in a long, slender string with a single row of eggs in parasitic forms attached on the surface of aquatic animals, as in Caligidae or in Pennellidae.

The shape of the egg strings is, of course, dependent on the number and size of the eggs in the egg string, but that does not give us the whole explanation of their variety in shape. Nor, if we examine the genital apparatus of the females, which has been minutely described by Rathke, Claus, Scott, Wilson, and others, do we find an explanation of this variation. There simply is no apparatus in connection or contact with the genital duct to shape the egg strings. The shape is entirely determined by the movements of the female and the pressure of the water. This can be seen clearly when in the early morning hours one observes the egg laying of one of the fish-parasite copepod females.

We will first look at a *Caligus* female with still empty egg strings attached to her genital openings and the oviduct filled with ripe eggs ready for fertilization and leaving the oviduct. The egg laying begins

with the ejection of a little secretion from the cement gland of the genital apparatus, which will detach the remaining empty egg capsules from the last hatch. At this time the *Caligus* female undergoes severe birth pangs, with violent convulsive contractions of the whole body, and the claws of the different appendages which are inserted in the skin of the fish deepen their hold in the flesh of the fish with convulsive grips. Suddenly a particularly violent contraction of the female's body and limbs ejects the eggs from a single loop of the oviduct. As a result of this, the very powerful claws, especially those on the second antenna by which the animal maintains its hold on the

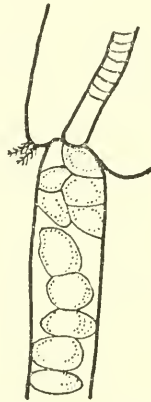


FIG. 1.—Egg string of *Caligus rapax* M. Edwards shed in captivity. The *Caligus* is attached to a cod placed in an aquarium. It can be seen that the eggs are not fully drawn out but are more irregularly arranged and therefore the cement is not shaping separate cases around each single egg.

host, are driven like spurs into the flesh of the fish. The fish feels this as a strong irritation and leaps forward in the water. Since the *Caligus* during this process is always fastened with its head pointing forward toward the head of the fish, this leap of the fish and the resulting resistance of the water will act as a backward-directed pull or drag on the newly laid egg masses covered by the freshly secreted and yet unhardened cement. The eggs are thus pulled out into a long string, like a string of pearls, before the secretion hardens. Furthermore, the pull is strong enough to separate the eggs slightly, which not only leaves space for a membranous cement partition between each egg, but also leaves a little empty space around the eggs. The membrane divides the egg string into a series of narrow compartments in each of which is a single egg which does not quite fill the

space between the partitions, thus leaving room for the subsequent development of the larva.

After the ejection of the eggs from a single loop of the oviduct, the spawning female rests for a few minutes, during which period peace also comes to the fish. In this period, however, vigorous peristaltic motions take place in the lower part of the oviduct through

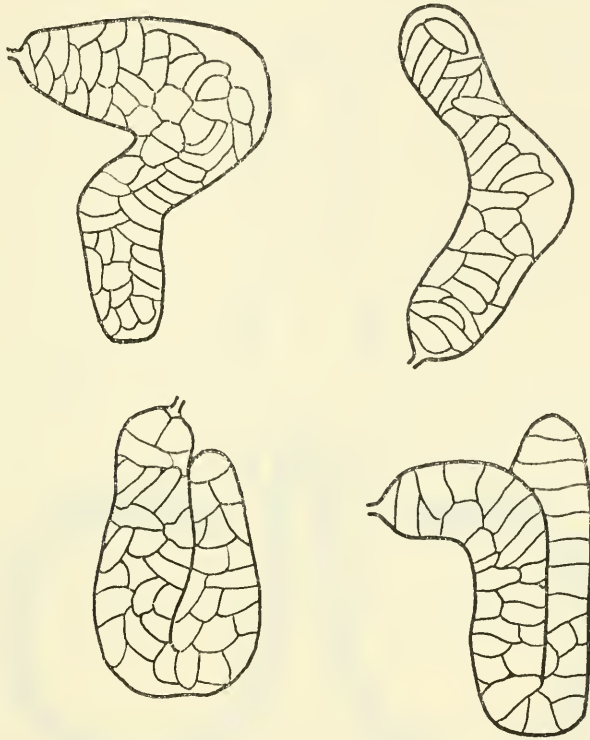


FIG. 2.—*Caligus curtus* (O. F. Müller). Egg masses shed in culture dishes of 8 cm. in diameter with air bubbling through. The irregular arrangement is clearly seen. Such egg masses will have no chance to develop.

which new eggs are pushed forward until they fill the last bend near the opening with eggs. New severe convulsive birth pangs eject a new group of eggs and again start the fish leaping forward in the water.

At the end of each egg-laying performance both the copepod and the fish are exhausted, resulting, especially in captivity, in weak leaps of the fish during subsequent egg layings. This in turn results in egg strings that are not fully drawn out, as shown in figure 1. In

Pennella the fast movement of the whales explains the long egg strings.

If the *Caligus* is not attached to a fish during the egg laying, but is placed in a dish, the egg masses, because of lack of pull, assume the peculiar appearance shown in figure 2.

In the gill parasites such as the Chondracanthidae, mostly living in the gill cavity of fishes, the water current is more constant, although

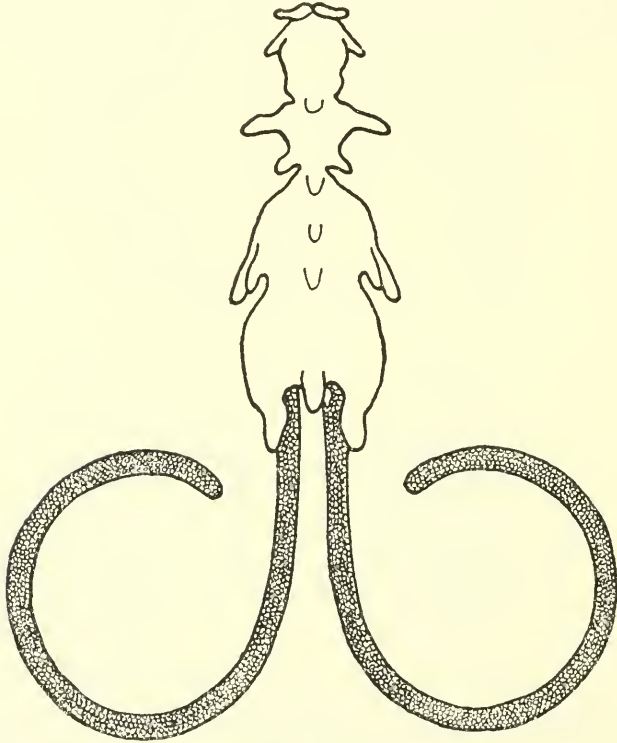


FIG. 3.—*Chondracanthus lophii* Johnston, female with egg strings.

the current will increase somewhat if the fish leaps as a result of being irritated by the copepod; because of these more vigorous movements the fish needs more oxygen and therefore more water passing the gills. In these gill parasites we therefore also find long, slender egg strings, not, however, drawn out into a single string of pearls, but a string several eggs thick (fig. 3).

The Lernaeopodidae have a fixed attachment and therefore are not able to irritate the fish. The shape of the egg strings in this case

is partly dependent on the activity of the fish species; therefore we find the egg strings shaped like long or short sausages.

Among the free-living planktonic forms the *Cyclops* is a clumsy fellow who makes only little speed with his relatively short antennae. The female in her birth pangs, therefore, only jumps around in small spirals and loops without any strong pull on the extruding eggs. The egg masses are drawn out a little before the cement hardens and are shaped into two oval bodies under the abdomen of the female.

In the Diaptomidae the antennae are long, slender, floating organs, too weak to provide any locomotion for the animal. In this case the thoracopods are the organs for locomotion, sending a propelling current of water backward. The fourth pair of thoracopods are long and reach nearly to the furca of the telson. Therefore when the eggs are ejected from the oviducts, the thoracopods will send a propelling current backward, circulating the extruding egg masses on the genital segment and producing a single globular egg ball such as is found in most Diaptomidae. In most calanids the cement gland is absent, and the eggs are discharged free in the water.

In most pelagic Harpacticidae the short antenna and thoracopods propel the animals forward, producing their egg-shaped to sausage-shaped egg strings. Among the sand dwellers of the Harpacticidae, we find small, irregular egg strings, partly shaped by the vacant spaces between the sand grains where the copepods are crawling.

These are a few examples to show how the shape of the egg strings of the copepods depends not only on the size and number of the eggs, but also on mechanical factors such as the method by which the copepod moves through the water and the speed of this movement.

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MECHANISM OF FEEDING IN HEMIPTERA

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Among the old works dealing with the mouth parts of Hemiptera are those of Davidson (1914), Grove (1919), Muir (1926), Myers (1928), and Becker (1929). Among the recent workers, the more important ones are Weber (1928-54), Rawat (1939), Snodgrass (1944), Butt (1943), and MacGill (1947).

The present studies were conducted in order to find out the individual and joint activities of the mouth parts and the processes involved in sucking the juices and injecting the saliva in the host tissue. This obviously necessitated the study of the skeletomuscular structure of each mouth part and the related areas of the head capsule as well as that of the endoskeleton of the head known as the tentorium. It was originally contemplated to select a large number of forms for such study so as to exclude the possibility of error of judgment. But as it was found that the fundamental makeup of many forms is identical, the author mainly devoted himself to the intensive study of the Indian mango hopper *Idiocerus niveosparsus* (Leth.) (Jassidae) and the Indian sugarcane leafhopper *Pyrilla perpusilla* Walker (Fulgoridae). The results were also checked by the study of the sugarcane white fly *Aleurolobus barodensis* Maskell. These studies are obviously important because Homoptera are vitally concerned in the spread of various plant diseases. They are also serious pests of a host of plants of extreme economic importance.

In Heteroptera the following types were studied:

1. *Sphaerodema annulatum* Fabr. (Belostomatidae).
2. *Belostoma indicum* Lep. Serv. (Belostomatidae).
3. *Anisops niveus* Fabr. (Notonectidae).
4. *Agraptocorixa hyalinipennis* Fabr. (Corixidae).
5. *Corixa promontoria* Distant (Corixidae).

HOMOPTERA

Head capsule.—The head capsule of Homoptera is characterized by a considerable development of the facial region as a result of its elongation due to opisthognathous mode of attachment. The labrum

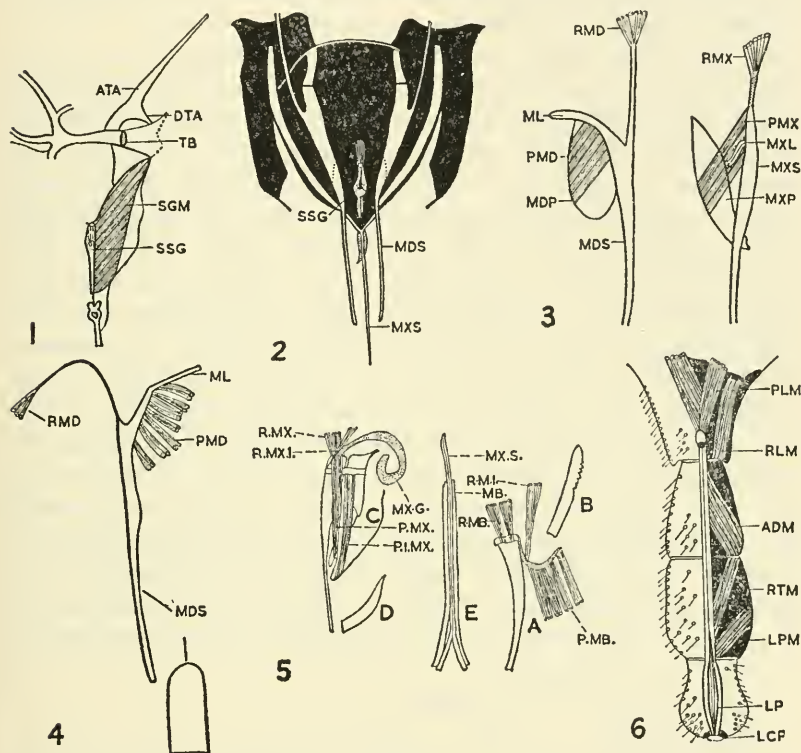
is a small triangular piece in *Idiocerus* as well as in *Pyrilla*. The clypeus is divided into a small anteclypeus and a highly developed postclypeal region in both insects. On the sides of the clypeus in case of *Idiocerus*, there is a maxillary plate which is divided by a longitudinal suture into two parts. The maxillary plate of *Pyrilla* is not divided by a longitudinal suture. Between the maxillary plates and the clypeus there is a plate which has been termed the mandibular plate by Weber and earlier workers and the lorum by Snodgrass and Butt. The nature of this plate is in dispute and according to some workers it is a part of the head capsule, having been demarcated from the clypeus. Snodgrass, however, regards it as belonging to the hypopharynx. According to the present writer, the loral plates are not identical in all the Homoptera. In *Idiocerus* they appear to be demarcated from the head capsule, and are external, while in *Pyrilla* they are derived from the hypopharynx and are internal.

Tentorium (fig. 1).—The tentorium of Homoptera has been described by Snodgrass, Muir, Myer, Weber, and Davidson. The present studies show that in *Idiocerus* the tentorium consists of a pair of 3-armed bars, and the central body of the tentorium is absent. In *Pyrilla* the tentorium is complete and consists of the central body lying closely approximated with the transverse maxillary bar and has three pairs of usual arms, dorsal, anterior, and posterior.

Mouth parts.—The hypopharynx of Hemiptera is a highly complex and well-developed structure. Its study has come into the limelight recently through the works of Weber and Snodgrass. It consists of a lobelike body lying below the clypeus. Basally it is continued into a pair of wings which are on their sides basally coalesced with the tentorium. Dorsally, at the junction of the anteclypeus, the hypopharynx is produced into a troughlike structure known as the sitophore, which forms the floor of the food canal. In *Pyrilla* (fig. 2) at its junction with the epipharynx the hypopharynx forms a pair of lateral plates, fused with the anteclypeus. Since the protractor muscles of the mandibular stylets arise from this plate, the author regards them as lora. On the ventral aspect of the hypopharynx there is the salivary syringe, which has an elaborate propelling arrangement consisting of a piston worked by muscles. The cavity of the syringe, as shown by Weber in *Pentatoma* and *Palonema* and as observed by the author in *Pyrilla*, is provided with a valve inhibiting the reverse flow of the saliva.

Epipharynx.—The epipharynx of Homoptera has been much neglected. Adequate attention to this structure has recently been given

by MacGill in *Dysdercus intermedius* (Pyrrhocoridae, Heteroptera). In *Pyrilla* the epipharynx is a well-developed plate whose lateral walls are highly sclerotized and are fused with the lora at their bases. The epipharynx and the hypopharynx jointly form the preoral part



FIGS. 1-6.

1. Tentorium of *Pyrilla*.
2. Mandibular and maxillary stylet and salivary syringe of *Pyrilla* in relation to the head capsule.
3. Maxilla and mandible of *Pyrilla*.
4. Mandible of *Pyrilla* with the apex magnified (oil immersion).
5. Mandibular and maxillary stylets of *Idiocerus*.
6. Labium of *Pyrilla* of which one-half is dissected.

of the food tube. The rest of the food canal is formed by the extension of the pharynx supported ventrally by the sitophore.

The salivary canal (salivarium) is formed by the extension of the median salivary duct which is elongated and runs along the ventral surface of the hypopharynx. It opens through a separate pointed spinelike process below the hypopharynx. In this way two perforated

canal-like structures are formed—one by the apposition of the pointed tips of the hypopharynx and epipharynx and the other by the elongated and tapering end of the common salivary duct. These points have not been carefully studied by the previous workers. It completely excludes the possibility of the mixing of the saliva and the sap sucked by these insects.

Maxillae (figs. 2 and 3).—The maxillae of Homoptera and also of Heteroptera consist of a maxillary plate and a stylet. The latter is joined with the plate by a weak, thin lever. The maxillary stylets are provided with double grooves on their inner faces, which form the suction and ejection canals of the bugs. At the base of each stylet there is a maxillary gland in *Pyrilla* as well as in *Idiocerus*. The maxillary gland is now widely known in Homoptera. There are two sets of muscles which bring about the movement of the maxillary stylets in *Pyrilla*, viz (1) protractors, which arise from the maxillary plate and are inserted at the base of the stylet, and (2) retractors, which arise from the dorsal wall of the head capsule, and are also inserted at the base of the stylet. In *Idiocerus* there are four muscles in relation with each maxilla. The first of them forms the retractors of the stylets which arise from the dorsal wall of the head capsule and are inserted at the base of the stylet. The muscles of the second set also arise from the head capsule and are inserted on the lever. They also help in the retraction of the stylet. The third muscle arises from the ventral extension of the gena and is attached to the base of the maxillary stylet. The fourth muscle arises in close proximity to the third and is attached to the lever. The third and fourth muscles are the protractors of the stylet.

Mandibles (figs. 3, 4, and 5).—The mandibles of Homoptera consist of a mandibular plate and a stylet. The stylet is connected to the plate with the lever. In *Idiocerus* these plates are demarcated from the genal region and are evidently not derived from the hypopharynx as stated in the case of *Cicada* by Snodgrass and Butt. The mandibular bristle is bilobed at the base. One of the arms is produced as an apodeme to which the retractor muscles are attached. The other is articulated with the lever which in its turn articulates with the base of the mandibular plate. The mandibles of *Idiocerus* are provided with three muscles. One of them is the protractor of the mandible and arises in close proximity to the maxillary muscle from the mandibular plate. The second and third muscles are the retractors of the mandibles. One of them is inserted on the lever and the other is inserted on the base of the stylet. In *Pyrilla* the mandibles are moved

by two muscles—namely, protractors—which arise from the loral plate near their junction with the mandibular plate. They are attached to the outer arm of the stylet. The other muscles are retractors and are inserted on the inner arm of the base of the stylet.

The labium of Homoptera is comparatively less well known. The works of special importance are those of Weber and Butt. In *Idiocerus*, the labium is 3-jointed with a basal gular plate. It is deeply grooved in order to lodge the stylets. At its base the labium is provided with a sclerotized plate which is produced posteriorly as an apodeme. It is bifurcated anteriorly. This plate provides the basis of attachment of the muscles of the labium and plays an important part in its movement. The apical segment of the labium in *Idiocerus*, as well as in *Pyrilla*, provides the clasping mechanism. In *Idiocerus* there is a pair of processes which form a sclerotized arch over the lateral groove. In *Pyrilla* (fig. 6) there are well-developed clasps in the form of hard pieces supported at their bases by the processes of the apical segment. The internal muscles of the labium consist of transverse or oblique fibers arising from the ventral wall in the region of the second segment and are helpful in deepening the groove of the labium and bringing about the clasping of the stylet. The external muscles of the labium consist of two sets. One of them arises from the head capsule and is inserted on the lateral plate. The other muscle arises from the apodeme of the labium and is inserted between the junction of first and second labial segments. The former works as the elevator of the labium and the latter as its depressor.

HETEROPTERA

Some salient features of the anatomy of the head capsule and mouth parts in Heteroptera are as follows:

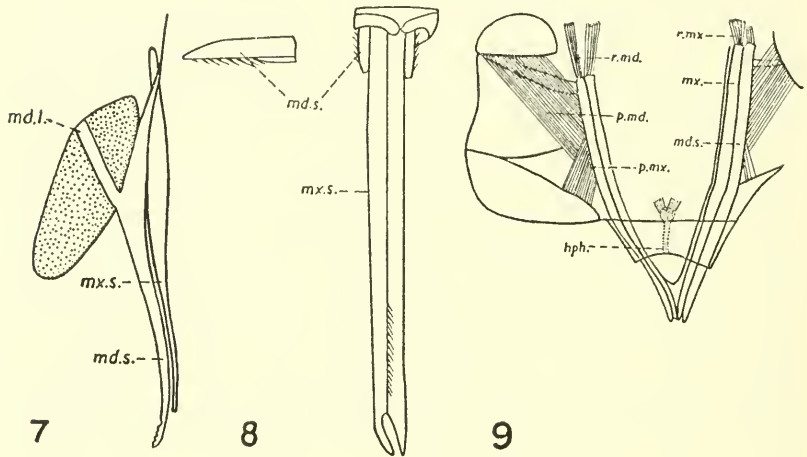
The dorsal wall of the head capsule in Heteroptera is neither frons (Becker, 1929) nor clypeus (Rawat, 1939, and Weber, 1954) but frons-postclypeus (Butt, 1943). In Coridae, however, frons and clypeus are separate.

The hypopharynx in Notonectidae and Corixidae is provided with rail-like ridges fitting in the maxillary stylets in order to give additional strength to their movements. Also there is a longitudinal groove to fit on a mandibular stylet ridge. These supports are extremely helpful in feeding.

Mandible (figs. 7, 8, and 9).—The mandibular stylet and lever are articulated with the head capsule. The mandibular stylets are shorter than the maxillary stylets and are provided with recurved spines at

their apices. The protractor muscle arises from the loreal mandibular plates, the retractor from the head capsule.

Maxilla (figs. 7, 8, and 9).—The maxillary stylet and maxillary plate constitute the maxilla. The stylets are long and are broad at their bases, which are continued into the back of the head capsule. The apex of a stylet is provided with interlocking hooks. The maxillary lever may or may not be present. A tubular gland opens at the base of each maxillary stylet as a rule.



FIGS. 7-9.

7. Mandibular and maxillary stylets of *Corixa*.
8. Mandibular and maxillary stylets of *Anisops*.
9. Mandibular and maxillary stylets and the hypopharynx with muscles of *Agraphocorixa*.

Mode of feeding in Hemiptera.—The apical segment of the labium is provided with a large number of fine sensory hairs. Inside this very segment the labial plate supports the stylets from below when the latter are moving into the wound. In addition to it, the rails and grooves on the sides of the hypopharynx maintain a fixed direction of the movement of all four stylets. Taking the stylets themselves it can easily be seen that the two maxillary stylets are interlocked and move together like the hypodermic needle of an injection syringe. The mandibular stylets can move along the sides of the maxillary stylets independently of each other. The procedure of the operation of the stylets at present accepted is that which has been proposed by Weber (cited by Snodgrass, 1944). According to this view the mandibles appear to be the effective piercing organs, and they work

alternately. At first, one mandibular stylet is thrust out and held in position, then the tip of the other comes down and meets it. The present writer (1949) has expressed doubt as to the validity of this explanation in the Indian mango hoppers *Idiocerus* (Jassidae) and *Pyrilla* (Fulgoridae). In the heteropterous bugs the views of the writer find further support. The mandibular stylets of these bugs appear to be adapted mainly for holding onto the tissue beneath the integument. The recurved spines on the outer aspects of their apices are amply suited for the same purpose. This having been achieved, the rest of the work of piercing the tissue to any required depth is performed by the needle formed by the interlocked maxillary stylets. The hairs on the sides of the inner aspects of each maxillary stylet provide a powerful mechanism for keeping the two stylets together. In *Anisops* (fig. 8) it can easily be observed that the maxillary stylets can travel to a great distance beyond the tips of the mandibles. The present writer has found the same feature in *Ranatra* (Nepidae) and *Sphaerodema*. The insertion of the protractor muscles directly on the main shaft of the maxillary stylet and the reduction of the lever furthermore prove that the maxillary stylets are indeed adapted to move to a far greater distance than the mandibular stylets in which protractor muscles are inserted on a well-developed lever. In fact the development of the lever in the mandibular stylet restricts the onward movement of the latter to a limited distance. In this connection it is interesting to note the length of the mandibular and maxillary stylets; those of *Sphaerodema* are obviously much longer than those of *Anisops*. The same feature has been described in *Naucoris cimicoides* by Becker as well as by Rawat. All these facts show beyond doubt that the maxillary stylets do not confine their movement to a distance enclosed between the two apices of the mandibular stylet as held by Weber, but that they move far beyond the apices of the latter. The present writer therefore holds that the mandibular stylets move only to a limited distance beneath the surface of the tissue to a desired depth so that the two stylets can catch the tissue by their recurved spines, which perform an anchoring function. The maxillary stylets which enclose the food and salivary canals move down to varying depths, performing the double functions of dissolving the tissue by means of salivary enzymes and sucking the fluid. The present view of the writer finds support from the observations of Awati (1914, fig. 25) on the potato capsid bug *Lygus pabulinus*. Awati has shown the movement of the stylets beneath the surface of the leaf. His figure clearly shows that the mandibular stylets catch

the tissue of the leaf, while the maxillary stylets have together moved down deep into the tissue. Puri (1924) has shown in the bedbug *Cimex* two similar structures at the apices of the maxillary and mandibular stylets, but he did not concern himself with the procedure of operation by different stylets.

ABBREVIATIONS USED ON THE FIGURES

<i>ADM</i> , abductor of labium.	<i>PIMX</i> , protractors of maxillary lever.
<i>ATA</i> , anterior tentorial arm.	<i>PMB</i> , protractors of mandibular stylet.
<i>DTA</i> , dorsal tentorial arm.	<i>PMD</i> , <i>pmd</i> , protractor of mandible.
<i>hph</i> , hypopharynx.	<i>PMX</i> , <i>pmx</i> , protractors of maxilla.
<i>LCP</i> , labial clamp.	<i>RLM</i> , retractors of labium.
<i>LP</i> , labial plate.	<i>RMB</i> , retractors of mandibular stylet.
<i>LPM</i> , muscle of labial plate.	<i>RMD</i> , <i>rmd</i> , retractors of mandible.
<i>MB</i> , mandible.	<i>RMI</i> , retractor of mandibular lever.
<i>mdl</i> , <i>ML</i> , mandibular lever.	<i>RMX</i> , <i>rmx</i> , retractors of maxilla.
<i>MDP</i> , mandibular plate.	<i>RMXI</i> , retractor of maxillary lever.
<i>MDS</i> , <i>mds</i> , mandibular stylet.	<i>RTM</i> , retractors of terminal segment of labium.
<i>Mx</i> , <i>mxs</i> , maxillary stylet.	<i>SGM</i> , muscles of salivary syringe.
<i>MXG</i> , maxillary gland.	<i>SSG</i> , salivary syringe.
<i>MXL</i> , maxillary lever.	<i>TB</i> , body of tentorium.
<i>MXP</i> , maxillary plate.	
<i>PLM</i> , protractors of labium.	

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STUDIES ON THE MOLECULAR ORGANIZATION OF INSECT CUTICLE¹

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(WITH TWO PLATES)

Specialists in the field have long recognized that the common idea of insect cuticle being composed basically of chitin is an inadequate description. It is probably incorrect too. As far back as the middle of the nineteenth century Berthelot suggested that cuticle was really a chitin-protein combination rather than a mixture. Various twentieth-century biologists and chemists have suggested that cuticle is a natural mucopolysaccharide or glycoprotein (see Richards, 1951). The general tendency among research workers in this field today is to think of cuticle as a glycoprotein that becomes modified and stabilized by sclerotization but which before sclerotization is relatively unstable. But there is no unambiguous *proof* that cuticle is a glycoprotein, and students of sclerotization usually ignore the chitin moiety.

In honor of Dr. R. E. Snodgrass, one of the great insect anatomists, we submit this little study of molecular anatomy of the cuticle. In this paper we will consider four related questions: (1) Are the protein molecules (arthropodin) sufficiently elongated to exhibit form birefringence? (2) What are the optically anisotropic units in normal cuticle, i.e., is cuticle optically simply a chitin-protein mixture or is there a chitin-protein optical unit? (3) Can the orientation of arthropodin molecules be deduced from optical analyses? (4) What are the relative orientations of chitin and arthropodin chains in insect cuticle?

MATERIALS AND METHODS

For pieces of cuticle with a high degree of orientation of micelles or crystallites, we used tendons (apophyses) from the legs of cockroaches (*Periplaneta* and *Blaberus*) and tarantulas. After gently

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tearing the membranes between the last two tarsal subsegments it is simple to hold the terminal piece and pull out the long tendon that extends from the pretarsal claws into the femur. This tendon may be examined in lateral view as a whole mount, either in saline solution or after any desired treatment.

For cross sections of the tendon, freshly dissected ones were cut with a freezing microtome and transferred from the cold microtome blade directly into 95-percent ethanol.

Arthropodin was extracted from isolated cuticles of nearly mature larvae of the fly *Sarcophaga bullata*. The larvae were eviscerated and the cuticles swabbed in three changes of cold distilled water over a period of 4 to 5 hours. The cuticles were then stored in 95-percent ethanol at 5°C. for several months. Extraction was with hot distilled water (90-95°C.) for 6 hours. The filtrate was evaporated to dryness and redissolved as needed. Artificial fibers were drawn manually from a viscous mass as it was drying.

Streaming birefringence was examined with a precision apparatus built on the concentric cylinder principle. The apparatus was made and is described by Kielley (1946). It is similar to the instrument used by Dainty et al. (1944). Sensitivity was increased by use of a Wratten green filter and dark-adapted eyes.

Quantitative determination of the birefringence of chitin is easy. One simply selects a tendon, purifies the chitin by extraction with hot NaOH solutions or other chemicals, measures the path length with a conventional ocular micrometer and the amplitude of birefringence with an appropriate compensator. We used Köhler rotating mica plates of $1/10$ and $1/22 \lambda$ maximum retardation and compensated to half extinction, i.e., matched the brightness of the tendon to the field (Bear and Schmitt, 1936). The magnitude of birefringence of chitin is then given by θ/d , where $\theta = 2m\lambda \sin B$. B is the measured rotation of the mica plate, λ is the "center of gravity" of white light (551 m μ), and m is the maximum retardation of the mica plate being used.

Quantitative determination of the birefringence of arthropodin is not so simple because good oriented alignment of molecules was not achieved in our drawn fibers (to judge from the fact that values calculated from them were much lower than values obtained by the next method). Since streaming birefringence studies showed that arthropodin exists in solution as considerably elongated particles, it follows that thin sheets dried on glass should have good orientation in the plane of the surface. However, orientation will be random

in that plane. If pieces are cut or broken from such thin sheets and examined on edge between crossed Nicols they are distinctly birefringent, and both amplitude and path length are readily measured. But, since orientation is random in the one plane, the measured extinction angle is only half maximum. Accordingly, one uses $\theta = 2m\lambda \sin 2B$ for the calculation. The necessary difference in calculation can be illustrated by a diagram.

In tendons purified for chitin one has the situation diagrammed in figure 1 A. Here regularly parallel micelles and microfibrils are readily oriented perpendicular to the beam of polarized light. A maximum effect is then obtained since the optic axis is parallel to the long axis of the fibers. In the thin sheets of arthropodin one has the situation diagrammed in figure 1 B. Here elongated molecules

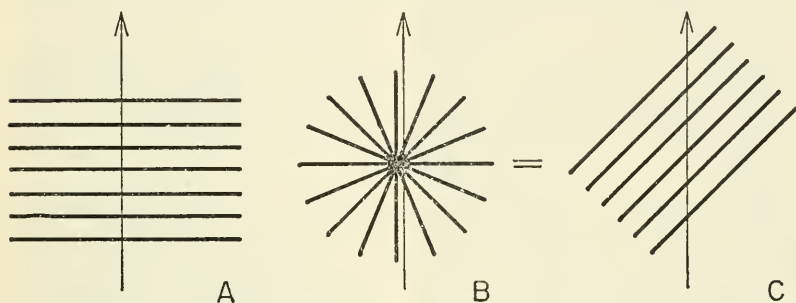


FIG. 1.—Optic axes and observational directions for tendons (A) versus thin sheets (B, C).

are all in one plane, but randomly oriented in all directions in that plane. Such a sheet is isotropic in surface view. When such a sheet is examined on edge, some molecules are being seen parallel to the light beam (and hence along their optic axis), some perpendicular to the beam, and others at all intermediate angles. The average value will be equal to that of regularly parallel micelles oriented at 45° to the light beam, as diagrammed in figure 1 C. Hence a correction factor of 2 must be added to the usual equation for calculation of magnitude of birefringence.

The refractive index of arthropodin was determined by the Becke line technique following immersion of drawn fibers in mixtures of a clear light mineral oil and α -bromonaphthalene. The determination was checked using pure chemicals (bromobenzene, *o*-toluidine, nitrobenzene, etc.). Dry and dehydrated tendons were examined in the same media. Hydrated tendons were examined in glycerine and in a saturated solution of KI (temp. 26 – 28°C .).

RESULTS

1. *The optical properties of extracted arthropodin.*—A moderately concentrated aqueous solution of arthropodin was examined at fairly low rates of shear.² A distinct but low flow birefringence was detectable, and could be verified as being true birefringence by cancellation on slight rotation of the analyzer. The amount of birefringence was much less than that of a myosin solution³ of roughly similar viscosity. Of more significance, the sign of birefringence was the same as that of the myosin solution (i.e., positive) and the angle of isocline was large but not as sharply defined. These data, crude as they are, show the presence of relatively large anisodiametric particles exhibiting form birefringence. The indefiniteness of the angle of isocline implies a somewhat heterogeneous mixture of particle sizes. Obviously, the optic axes of the particles are the long axes.

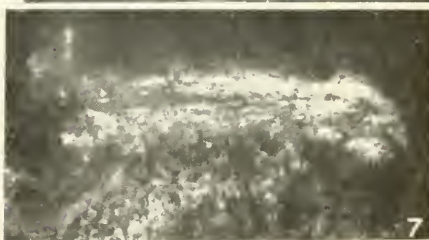
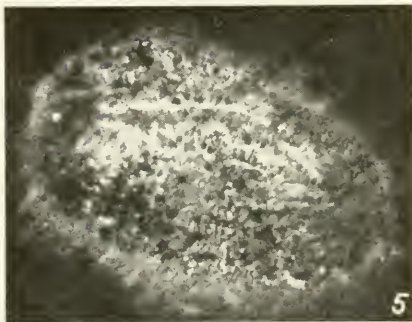
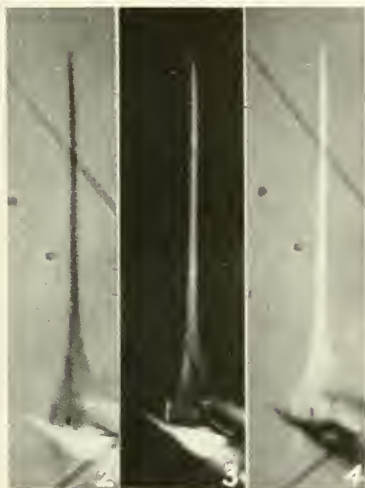
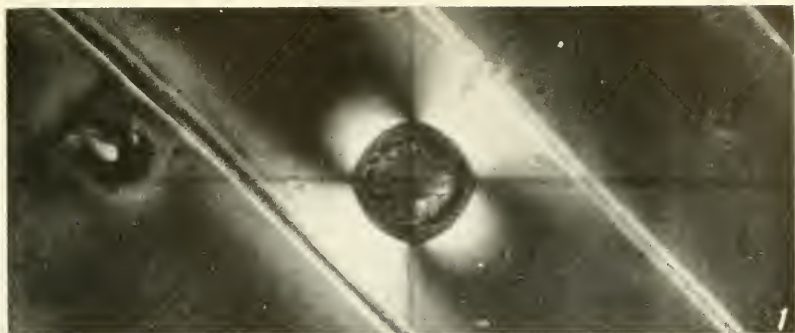
From the above data one would expect the solutions to give a strong Tyndall effect. Examination normal to a beam of light in a dark room shows considerable scattered light which is highly polarized. As performed, this only confirms the presence of sizable particles in the solution.

Thin dried sheets of extracted arthropodin are completely isotropic in surface view. But if the layer dried onto a slide is rather thick it will develop ridges during drying. Occasionally an air bubble will be trapped in such thick films. Both the ridges and the air bubbles set up strains during the final stages of drying such that orientation and hence birefringence is evident along or around each (pl. 1, fig. 1). If a drop of solution is allowed to dry on a microscope slide under continuous observation, a stage is reached just before complete dryness when fibers can be drawn manually from the viscous mass simply by stirring it with a needle and then withdrawing the needle. Such fibers are of various diameters; most of those drawn were in the range of 5 to 50 μ . Between crossed Nicols these fibers exhibit birefringence which is of positive sign relative to the long axis of the fibers (pl. 1, figs. 2-4). That this is indeed birefringence, and not an artifact due to surface reflection or diffraction, can be shown by rotation of the mica plate compensator which produces extinction or intensification.

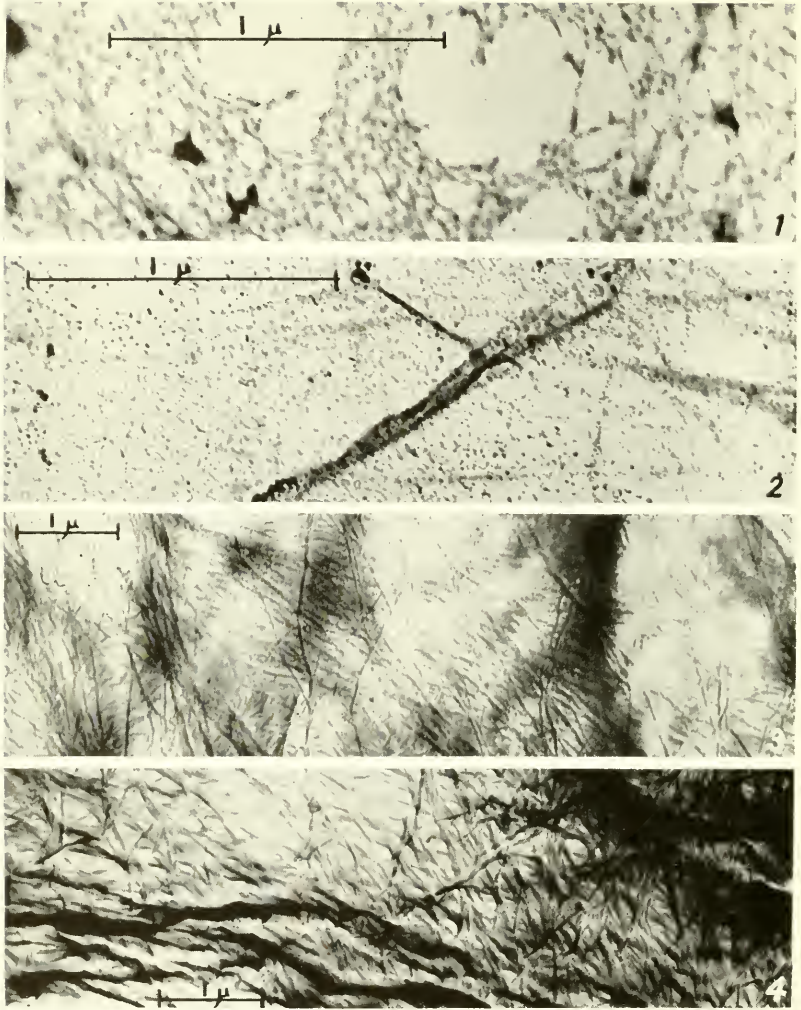
Immersion of air-dried sheets or fibers of arthropodin in media of

² In the absence of information on molar concentration, viscosity, etc., one can only make general qualitative statements from flow birefringence. The solution used contained the extracted arthropodin from about 100 cuticles in 2 ml. of water.

³ Chicken leg muscle extract made with 0.5 M KCl at pH 6.5.



1, Thick sheet of air-dried arthropodin with ridges and trapped air bubble, viewed in polarized light between crossed Nicols. 2-4, Large artificially drawn arthropodin fiber which tapers from about 50μ to 15μ at the tip. Crossed Nicols: compensated to extinction (2), uncompensated (3), and compensated to maximum brightness (4). Cross hairs partly visible as oblique lines. 5, Cross section of normal cockroach tendon ($100 \times 150\mu$). Brightest along lumen. Crossed Nicols, no compensation. 6, Another cross section at smaller part of tendon ($40 \times 120\mu$) showing clear lumen. Crossed Nicols, no compensation. 7, Portion of another cross section showing great intensity parallel to surface of elongated lumen. Crossed Nicols, no compensation. 8, Oblique and cross sections from the same field to show relative intensity of birefringence (intervening area from this print cut out to save space).



1, High-magnification electron-microscope picture of particles that may be chitin micelles in a partly decomposed air-sac (tracheal) membrane. 2, High-magnification electron-microscope picture of a granular membrane (granules-micelles?) showing alignment of particles leading to formation of microfibrils. Material transformed to chitosan and stained with $ZrCl_4$. From ecdysial membrane of a moth pupa (Richards, 1955). 3, Lower-magnification electron-microscope picture of clear chitin microfibrils from pepsin-digested ecdysial membrane (Richards, 1955). 4, Adlineation of microfibrils into larger fibrillar bundles in membrane purified to chitin with hot 10-percent NaOH.

various refractive indices produced no noticeable change in the amplitude of birefringence. This was somewhat surprising since the demonstration of streaming birefringence implies that at least a sizable portion of the birefringence is form birefringence (i.e., birefringence due to the shape of the molecules). These data show that the arthropodin molecules either exhibit largely intrinsic birefringence (i.e., birefringence due to the internal structure of the molecules) or, more likely, that the packing of arthropodin molecules in air-dried sheets and fibers is so tight that the organic immersion media could not penetrate between the molecules. For reasons to be detailed later, we conclude that anhydrous organic molecules of moderate size do not penetrate into dry arthropodin. Similarly, saturated aqueous solutions of potassium iodide (in which arthropodin is insoluble) have no effect and hence, presumably, do not penetrate.

2. *The optical properties of cuticle.*—It has been known for many years that the birefringence of any cuticular structure (tendons or setae are usually studied) increases on purification of the chitin in the structure. The initial objective of the present study was to see whether or not the birefringence of normal cuticle is a simple arithmetic sum of the birefringence of its chitin and arthropodin components.

Determination of the magnitude of birefringence shows that chitin is some 6 to 7 times as strongly birefringent as arthropodin. With specimens immersed in ethanol, and 9 separate determinations of the magnitude of birefringence of chitin from purified leg tendons of a tarantula, 7 determinations from normal leg tendons of cockroaches (*Blaberus*), and 6 determinations from thin sheets of arthropodin, we obtained the following average values:

Chitin	0.00084
Cuticle	0.00070
Arthropodin	0.00013

One may object to the above materials coming from three widely different arthropods. But there is no reason to think that the extra labor involved in obtaining all these from one source would change the values significantly. The highly purified chitin of tarantula tendons was used because it was already prepared and of tested purity. A large volume of literature attests the uniformity of chitin within the phylum Arthropoda (Richards, 1951; Rudall, 1955). Arthropodin is somewhat heterogeneous even in the extract from a single species as shown by Hackman's (1953) separations and by the somewhat indefinite angle of isocline we found in our flow birefringence determination. But it is doubtful that these known differences would have

a large effect on the birefringence values. Within the time available it was not feasible to dissect and extract sufficient tendons to make a determination on arthropodin from tendons. Instead, as a check on this point, the amplitude of birefringence of cockroach tendons was measured at marked points before and after various treatments. The same values were obtained for fresh tendons in ice-cold water and in absolute ethyl alcohol, and from rewetted tendons after drying. However, an abrupt rise of some 25 to 35 percent followed extraction of the tendon with either hot water or hot 10-percent NaOH solution. This change is qualitatively what would be expected from the separate determinations for chitin, cuticle, and arthropodin given above. The fact that the change was about twice as large as anticipated may or may not be significant.⁴ It may only be a reflection of the fact that soft cockroach cuticle has about twice as much protein as chitin (Den- nell and Malek, 1956; Pfaff, 1952; Tsao and Richards, 1952).

It is obvious from inspection of the above values that the birefringence of cuticle can be accounted for by combination of the chitin and arthropodin values *only if* the arthropodin value is subtracted from the chitin value. But the sign of the birefringence value is positive for both chitin and arthropodin. Therefore, two possibilities exist: (a) the chitin and arthropodin molecules are combined into a complex which itself acts as an optical unit, or (b) the chitin and arthropodin molecules are oriented at right angles to one another (fig. 2 B). Even with some uncertainty as to the accuracy of the value given for arthropodin, the close agreement of the cuticle value to the chitin minus arthropodin value favors the second possibility.

It is well known that the optic axis of chitin is the "b" axis of the crystal lattice, which is the same as the long axis of the chitin chains and the long axis of tendons (Richards, 1951). In other words, a tendon purified to chitin is strongly birefringent when viewed from the side but isotropic when viewed in cross section. But if arthropodin molecules are normally arranged in some regular manner at right angles to the chitin chains, a cross-sectional view of a normal tendon should not be isotropic. Examination of fresh cross sections of cockroach tendons cut on a freezing microtome and immediately placed in absolute ethanol are birefringent (pl. 1, figs. 5-7). Transferring

⁴ Illness and the imminence of deadline date for submission of this manuscript precluded repeating these determinations on an adequate number of preparations. Of the two determinations made, one showed a 25-percent rise, the other a 33-percent rise, the lower value probably being more accurate than the higher one.

such sections to hot 10-percent NaOH solution for 20 minutes abolished the birefringence, i.e., cross sections became completely isotropic. This is strong evidence—it could, indeed, be called proof—that the arthropodin particles in normal cuticle are oriented at a right angle to the chitin chains.

Incidentally, as was to be expected from the magnitude values given above, the birefringence of a cross section of tendon is much lower than the birefringence of a longitudinal section. This is shown by

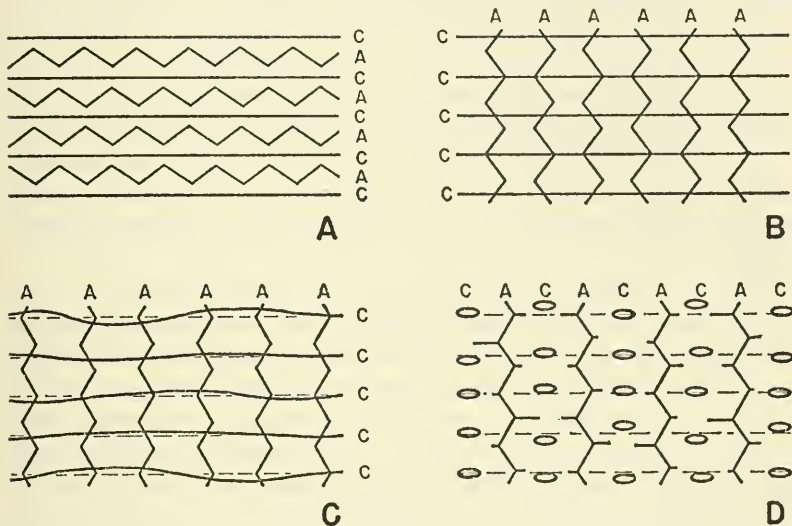


FIG. 2.—Diagrams of chitin and arthropodin chains. Chitin molecules drawn as straight lines, arthropodin molecules drawn as zigzag lines. A, The parallel chain suggestion of Fraenkel and Rudall (1947). B, The cross-grid possibility listed by Rudall (1950) and verified herein. C, The distorted cross grid proposed herein; viewed along the *c* axis. D, The same, but viewed along the *b* axis.

relative brightness of the low magnification pictures of a cross section and a longitudinal section of normal tendon presented in plate 1, figure 8. If one could be sure that the sections were of the same thickness, they would permit ready determination of accurate values for the birefringence of chitin, arthropodin, and cuticle. But, since the thicknesses of our sections were probably only approximately the same, we can only say that the value for longitudinal sections is a number of times greater than that for cross sections and approximately what one would expect from the numerical values given in preceding paragraphs.

One further fact can be determined from these cross sections. These cockroach tendons are really greatly elongated apodemes, that is, hollow invaginations of the body wall. As such they have a distinct lumen of elongated elliptical shape in cross section. Hence there is a recognizable "surface." Rotation of the stage of the microscope results in brightening and darkening the cross sections, the greatest brightness occurring when the long axis of the elliptical lumen is at a 45° angle to the Nicols (pl. I, fig. 7). It follows that, as one would expect, the long axes of the arthropodin particles are probably parallel to the cuticle surface. Therefore we can say that the arthropodin particles most likely extend between chitin chains along the a axis of the unit cell. Presumably herein lies the explanation of the cuticle micelle having axis dimensions $b > a > c$ (Fraenkel and Rudall, 1940). The great length of the b axis of the micelles is related to the length of chitin chains, the length of the a axis to the length of arthropodin chains, and the shortness of the c axis to the average number of aligned chains.

3. *The imbibition of cuticle, arthropodin, and chitin.*—In the course of studies of chitin birefringence various authors have commented on the desirability or even, in some cases, the necessity for purifying the chitin, i.e., removing the other components, before success can be had in obtaining an imbibition curve where amplitude of birefringence is plotted against refractive index of the immersion medium (e.g., Castle, 1936; Lees and Picken, 1945; Picken and Lotmar, 1950). We find this to be a property associated with the protein arthropodin.

It is simple to measure the refractive index of air-dried fibers or films of arthropodin by the Becke line technique, but we had no success in attempting to determine the R. I. from the minimum of an imbibition curve. With the Becke line technique and a series of mineral oil-bromonaphthalene mixtures, the R. I. was found to lie between 1.552 and 1.555 but to be definitely closer to the latter. This value was not noticeably altered by oven-drying at 105° C. Immersion of dry fibers in a series of C.P. fluids of known R. I. gave similar results. Accordingly we can say that the R. I. of dry arthropodin is close to 1.554. This value is close to the R. I. of both chitin and silk (Richards, 1951) but is considerably higher than the values recorded for waxes of insect cuticles, for collagen, and for insect connective tissues such as the basement membrane and neural lamella.

While the fibers and films can be made virtually invisible (except for their light absorption—they are a light amber color) in media of R. I. 1.55 to 1.56, the birefringence is not measurably altered even

when a sensitive Brace-Kohler compensator is being employed. In fact, plate I, figures 1-4, were made from dry arthropodin immersed in the oil-bromonaphthalene mixture of R. I. 1.555 to eliminate refraction and hence give better photographs.

When we found that the amplitude of birefringence of dried arthropodin fibers was independent of the refractive index of the immersion medium, the possibility existed that these molecules were intrinsically birefringent. Alternatively they would have to be impermeable to the medium since the working distinction between form and intrinsic birefringence is the abolition of the former in media of the same refractive index as the substance. The birefringence of chitin is known to be largely of the form variety (Richards, 1951). If the birefringence of arthropodin is intrinsic, and if the arthropodin molecular chains are at a right angle to those of chitin, then a reversal of sign of birefringence should occur on successful imbibition of a normal tendon. Tests showed no effect from immersion in the organic media customarily used for these determinations even if the media were heated and the specimens left immersed for several days. But these anhydrous organic compounds require preceding dehydration either by drying or by absolute ethanol or other agents. With dehydration the lattice apparently tightens up so much that the media do not penetrate. Tearing the tendons shows that the nonpenetration is not due to any surrounding membrane or sheath.

We did not have any mercuric iodide available, but a saturated aqueous solution of potassium iodide has a fairly high refractive index (>1.50). Immersion of fresh tendons in saturated aqueous potassium iodide reduced the amplitude of birefringence by 60 to 70 percent; immersion in pure glycerine (R. I. = 1.47) reduced the amplitude about 50 percent. Drying this tendon with alcohol and passing into xylol (R. I. = 1.50) returned the amplitude approximately to the original value. Air-drying from xylol followed by immersion in sat. aq. KI produced no noticeable change. It follows that it is only the hydrated cuticle which is freely permeable. In contrast, tendons and setae purified to chitin are freely permeable (Picken, 1949, and others). Therefore, the impermeability of dry cuticle is due to arthropodin, and dry arthropodin is impermeable both by itself and when associated with chitin in cuticle.

Of more interest to the subject of the present paper, the large reduction in birefringence on immersion of hydrated tendons in sat. aq. KI, and failure to obtain reversal of sign of the tendon, implies that the birefringence of arthropodin is at least largely a form birefrin-

gence. This is as it should be to obtain a measurable positive birefringence of flow.

One seemingly anomalous result we are not prepared to explain is that air-drying from water produces a decrease in amplitude of birefringence of about 50 percent. The original value is regained on rewetting with distilled water.

DISCUSSION

If an optical unit had been found in normal cuticle that was not explainable as simply an arithmetic sum of the chitin and arthropodin values, this would have been strong evidence for cuticle being a good glycoprotein. Since to a first approximation the magnitude of cuticle birefringence does equal the value of chitin minus the value of arthropodin, the optical data tell nothing about any possible glycoprotein linkage.

Nonetheless some form of chitin-protein linkage seems inescapable, but it must be a very weak linkage. Fraenkel and Rudall (1947) obtained good chitin crystallites after steam treatments, repeated wetting and drying, or grinding cuticle to a powder in water. Various authors have found microfibrils by electron microscopy (pl. 2, figs. 3, 4) only after treatments with acid, alkali, digestive enzymes, oxidizing agents, or hot water, all of which disrupt or remove the arthropodin (see Richards, 1958). Recently, Sanborn and Young (in press) stained protein fibrils in cuticle sections but they, too, had to use a pretreatment with butyl alcohol which is thought to disrupt glycoprotein bonds. Using a different type of approach to the problem, Hackman (1955a) showed that acetylglucosamine can be made to react with arthropodin, and that some protein can be adsorbed from solution by purified chitin. The ease with which the protein could be eluted from chitin agreed with other data in implying a very weak bonding—less strong than a hydrogen bond and hence likely some type of induced dipole attraction.

We cannot imagine the chitin and protein both being oriented in a definite relation to one another unless some bonding is involved. We have demonstrated such orientation by these birefringence studies. Also, oriented proteins have already been reported in cuticles from X-ray diffraction data but without demonstration of a constant relationship between the orientation of chitin and protein (Picken and Lotmar, 1950). Although no one has yet positively identified a glycoprotein bond in cuticle, we consider that documentation of a regular

crossed-grid structure necessitates postulating the existence of such a bond, and hence of a chitin-protein entity during cuticle development.⁵

Fraenkel and Rudall (1947) have listed the X-ray diffraction characteristics of normal dry cuticle. These include sharpness of the *b* reflections, diffuseness of both the *a* and *c* reflections, and the presence of a 33 Å spacing perpendicular to the cuticle surface, the latter being increased by 50 percent or more on wetting with water. The *a* and *b* axes are parallel to the cuticle surface, and the side chains of the chitin molecules are perpendicular to the cuticle surface. On a basis of similarity of the X-ray diffraction repeat distance in extracted arthropodin with the length of a chitobiose unit, they suggested a parallel arrangement of chitin and arthropodin chains similar to that diagrammed in figure 2 A. Subsequently, in a symposium paper that is probably unknown to most entomologists, Rudall (1950) did point out that the variability in side chain spacings of the protein chains makes it conceivable that the protein might form a crossed-grid arrangement with the chitin chains. Since we have now demonstrated the existence of some kind of a crossed system it seems likely that chitin and arthropodin chains in cuticle are normally each weakly cross-linked by the other. In soft cuticle the protein is readily displaced or removed. On hardening of the cuticle by sclerotization there is an addition of other compounds, dehydration, desalting (Richards, 1956), and stabilization of the protein (Richards, 1958; Wigglesworth, 1957). We have no idea yet whether this stabilization involves linkages to chitin chains as well as to the arthropodin chains, but, in any case, a stabilized crossed-fiber grid will be produced. Such grids break but do not tear readily (sclerotized setae break irregularly but, after removal of the protein, split [Lees and Picken, 1945]).

The details of how the crossed arthropodin and chitin chains are to be fitted together remains to be determined. Clearly the chitin chains extend in the *b* direction and the arthropodin chains in the *a* direction. But insertion of the arthropodin chains does not produce any regular displacement of chitin chains; it makes the *c* reflections diffuse rather than larger. Otherwise stated, the arthropodin chains must modify the chitin lattice only at some points, not at all points. There results, then, a mixture of chitin spacings and variously modified chitin spacings

⁵ Since the above was written, Foster and Hackman (1957) have published a note reporting a strong co-valent bond between chitin and protein in the crab, *Cancer pagurus*. Interesting and important as this is, it can represent only a part of the full story because their glycoprotein contained less than 5 percent protein whereas insect cuticles usually contain 1 to 2 times as much protein as chitin (Richards, 1951).

without the appearance of a sharply defined new spacing (except the larger 33 Å spacing treated below).

But insertion of the arthropodin chains parallel to the (001) plane (=parallel to the a axis) does not automatically account for diffuseness of the a axis itself. Somehow spacings must be distorted in this direction also. One of the striking features of arthropodin is its high percentage of large side chains (phenyl, carboxyl, and heterocyclic groups). Whereas silk fibroin is composed of about 90 percent simple amino acids, arthropodin has only about 50 percent simple residues (Duchateau and Florkin, 1954; Johnson et al., 1952). With so many large side groups the arthropodin molecules must be very lumpy chains. This composition is presumably important to cuticle development but it would be expected to produce considerable irregularities in molecular lattice spacings. If we assume that these side groups (like the side groups of the chitin chains) project in the c direction, then distortion giving diffuseness along the a axis is understandable.

Such orientation with resulting distortion in both a and c axes is diagrammed in figure 2, C and D. For those unaccustomed to plane diagrams a three-dimensional construction of the chain arrangements and postulated distortions is presented in figure 3.

The above is not the only way diffuseness could be produced in both the a and c directions, but it seems the simplest postulate and adequate for existing data.⁶

The preceding discussion omits consideration of the 33 Å spacing perpendicular to the cuticle surface. This is the spacing that increases greatly when the cuticle swells on being rewetted with water. Allowance will have to be made for variable spaces for water molecules largely limited to this axis (the c axis). But even without allowing for swelling by water it is not at all obvious what or how many units need to be added to produce a 33 Å spacing which includes the 19.25 Å of the c axis of the chitin unit cell.

Another enigma that likewise must await further study is what happens in cuticles where the chitin content is low or undetectable (absent?).

Finally, demonstration that arthropodin chains extend perpendicular to chitin chains makes it seem less surprising that most workers

⁶ For instance, one could postulate more complicated situations such as some or even all of the arthropodin chains extending obliquely through the chitin unit cell (e.g., in the (111) plane), or one could think in terms of helical coils. Another possibility suggested by the recent paper of Parker and Rudall (1957) is that the arthropodin particles really represent folded protein chains.

have failed to detect microfibers by electron microscopy in normal insect cuticle (Richards, 1958). Microfibers become visible in the electron microscope after treatments which disrupt or remove the protein. Aggregates that presumably represent chitin micelles (pl. 2, fig. 1) and seem to align (pl. 2, fig. 2) to give microfibers which in turn associate into larger fibers (pl. 2, figs. 3, 4) have been treated in

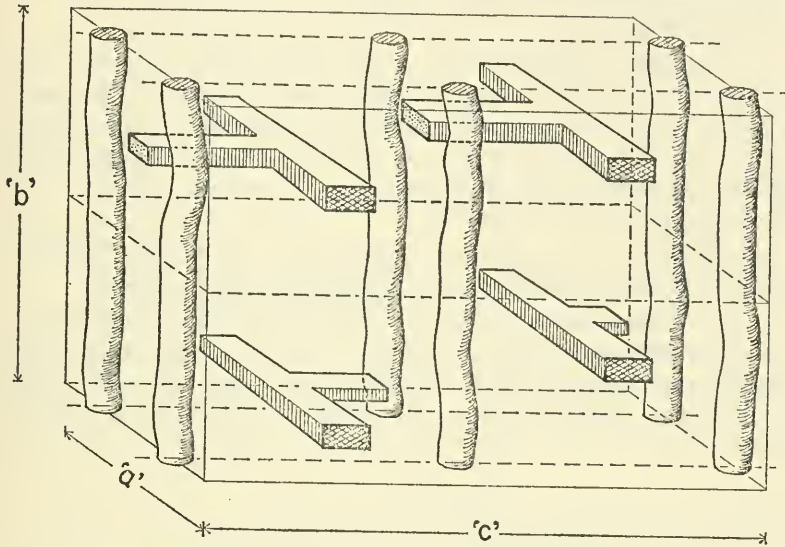


FIG. 3.—Three-dimensional reconstruction of cuticle lattice with a , b , and c axes indicated. Chitin chains drawn as irregularly displaced cylinders, the arthropodin chains as rectangular bodies with side groups of various sizes.

some detail by Richards (1955). One would expect the aggregates and small microfibers to be more or less masked by cross-bonding protein chains. Such a masking effect should become less with increasing fiber size. Accordingly, one should not be surprised to observe the large fibers called "Balken" in normal cuticle and yet fail to find the small microfibers until their contrast is augmented by protein removal. At present, however, this is only a logically satisfying guess—whether or not it is true remains to be proved.

The more gross aspects of cuticle organization, notably the microscopically visible laminar structure, can only be speculated about at present. It seems quite reasonable to suppose that these originate from competitive depositions (Picken, 1949) or from energy troughs in electrostatic fields (Richards, 1951), but data simply do not exist for making any objective choice among conceivable mechanisms.

SUMMARY

1. The elongated molecular chains of arthropodin are oriented perpendicular to the chitin chains in normal insect cuticle. The result is a cross-grid arrangement (figs. 2 B-D, 3) with both protein chains and chitin chains parallel to the cuticle surface.
2. The optical properties of cuticle are at least approximately an arithmetic sum of the optical properties of the component chitin and arthropodin chains.
3. Extracted arthropodin has a refractive index of about 1.554. In aqueous solution it consists of particles large enough to produce a Tyndall effect and elongated enough to show flow birefringence. Drawn fibers are also birefringent. The birefringence is positive relative to the long axis of the particles and is at least largely a form birefringence.
4. Values for the magnitude of birefringence were determined as: Cuticle=0.00070, chitin=0.00084, and arthropodin=0.00013.
5. The impermeability of dried cuticle is due to the arthropodin.
6. The influence of these findings on current concepts of cuticle organization is discussed. The data do seem to rationalize the failure to find microfibrils in electron-microscope pictures of normal insect cuticle.

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METACHEMOGENESIS—POSTEMERGENCE BIOCHEMICAL MATURATION IN INSECTS¹

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In April of 1946, with the resumption of my graduate studies at the University of Minnesota after almost 4 years' absence, I was fortunate in being able to enroll in a course in insect morphology being given by Dr. R. E. Snodgrass, who was visiting professor in entomology at that university at the time. This first meeting with Dr. Snodgrass marked the beginning of a professional and personal acquaintanceship that has persisted through the past dozen years. His skillful interpretation of anatomy in functional terms imparted a dynamic and vital significance to the otherwise cold details of insect body structure. As a physiologist by earlier training and primary interest, I was especially stimulated by Dr. Snodgrass's deductions concerning function and phylogenetic implications from his careful observations. The theme of this contribution represents certain inferences from experimental observations of a nonmorphologist about a biological phenomenon, metamorphosis, in which Dr. Snodgrass has long been demonstrably interested. It is therefore a distinct privilege for a physiologist, like myself, to engage in this labor of love—the participation in a volume dedicated to the foremost morphologist of our time.

THE PHYSIOLOGICAL APPROACH

Without question science is today witnessing a rapid increase in the mutual participation of relatively unrelated disciplines of research, heretofore considered exclusive by the very nature of their accustomed research methods. In the biological sciences such exclusiveness is more often than not based upon the particular conceptual approach and ratiocination processes of the scholars of each of the specific areas involved, from taxonomy to physiology. For reasons particularly apparent to the scholars in such fields, but chiefly because of the unavailability of other techniques or research procedures, students of

¹ The author is deeply appreciative of the conscientious, patient, and understanding help of Mrs. Elaine S. Rockstein in the preparation of this manuscript.

taxonomy and phylogeny have relied upon anatomical, histological, or gross morphological criteria, to the relative exclusion of biochemical or even biophysical methods, in separating taxonomic categories and in making phylogenetic deductions. More often it has been the comparative physiologist or biochemist who has recognized the potentiality of applying his own experimental data to interpretations in these other areas of biology.

In the case of the present writer, fairly specific interests and objectives have led him to observe that the techniques of the physiologist, especially biochemical methods, can be employed to advantage in the attack upon general problems in divisions of biology commonly referred to as "descriptive." For example, in an earlier study, Ford (1941, 1942, 1944), a geneticist with a primary interest in the physiology of gene action, observed that the distribution of different pigments among the members of one of the largest and most diversified of the lepidopteran families, the Papilionidae, followed a pattern of classification almost identical with that previously established upon structural considerations. Thus, by the use of simple chemical tests for separating different kinds of white and of red pigments, he confirmed the established taxonomic position of almost 370 different species of papilionid butterflies, with the exception of several species, the reclassification of which he recommended on the basis of his own chemical and previously described (aberrant) structural features. More recently Micks and Ellis (1952) and Clark and Ball (1952) applied the sensitive analytical techniques of paper partition chromatography to qualitative and quantitative amino acid estimation in hemolymph and total body amino acid content, in different species of mosquitoes. The former authors found a striking similarity in amino acid composition of adult female *Culex pipiens* Linnaeus and *C. quinquefasciatus* Say (thought by some to be subspecies). Clark and Ball compared the amino acid composition of the latter species and were able to separate it from *C. tarsalis* and *C. stigmatosoma* on the basis of qualitative differences in such amino acid content. Rockstein and Kamal (1954) have also evaluated the taxonomic position of six different species of flies, by the qualitative and semiquantitative estimation of different digestive enzymes in the alimentary tract of their larval forms; they also interpreted the data obtained in terms of adaptation by insects with different food habits from scavenger to obligate parasite.

The writer's interest in the physiological approach to the phenomenon of metamorphosis, especially in holometabolous insects, arose

from the apparent implication of his own experimental data and those of others interested in the biochemistry and physiology of such insects at different stages of their life histories. Dr. Snodgrass's response to a preliminary draft of this thesis included a comment that this suggested a "new line of research" in the matter of the continuity of development from the pupal stage into adult life (Snodgrass, personal communication, 1955). The scattered and sometimes obscure data presented herein will serve to emphasize the need for serious reexamination of the more classical, restricted concept of metamorphosis, as a climactic event by which the adult form is completed (aside from sexual maturation) at the moment of or very shortly after emergence of the imago. Indeed, there appears to be increasingly convincing evidence for the universal existence of postemergence maturation changes (such as alteration in biochemical properties) in adult holometabolous insects, which must be reflective of the maturation of specific body functions of the adult, such as flight ability, for example.

THE MEANING OF METAMORPHOSIS

In his classical treatment of holometaboly, Poyarkoff (1914) inferred that the pupa of holometabolous insects is not a recently acquired additional stage, interposed between the larva and adult, but is rather a subdivision of the imaginal stage, resulting from the interposition of an additional moult. It is interesting that he compared the pupa of the Holometabola with the subimaginal form of the Ephemera and suggested that they both represented incomplete adults. Hinton (1948) in confirming Poyarkoff's view also emphasized Poyarkoff's suggestion that this additional moult is essential to the completion of development of the adult in providing a new cuticle to which the muscles of the imago, newly formed, can attach themselves. Snodgrass (1954), in reaffirming this position, presents firm morphological evidence in the form of various examples of pupal resemblance to the adult. Wigglesworth (1954) also states that the obvious function of the pupa is to bridge the morphological gap that exists between the larva and the fully developed adult, for which he cites experimental embryological data (such as the fact that irradiation of the egg of *Drosophila* or of *Tineola* up to a particular point in embryonic development affects only larval characters; after such times only the imaginal characters may be affected). This is further evidence for the continuity of development of the adult from the larval stage, in the very presence of the imaginal discs in the general epidermis of the larva, frequently in the early instars, even in the prelarval embryo.

Snodgrass himself has stated (1956) that "a 'legless' fly maggot has legs (of the adult) developing in pouches of the skin covered by the cuticle," just as the wings of a grasshopper nymph are developing externally. Snodgrass also suggested (1954) that, rather than consider "metamorphosis" the transformation of the larva into an adult, the true metamorphosis in the life history is that "which has transformed the young butterfly into a caterpillar." This he considers a recent acquisition independently arisen among different orders of insects (and, therefore, with no phyletic significance), completely dissimilar from the primitive metamorphosis of other closely related invertebrates like annelids and crustaceans.

Nevertheless, many contemporary entomologists still consider metamorphosis in holometabolous insects as the transformation from the larval to the imaginal stage through the interposition of an additional stage, the pupa. The variety of evidence presented in this paper serves to support the concept of Poyarkoff of the pupa as a subdivision of the imaginal stage, by showing the continuity of the pupal and imaginal stages in the form of postpupal maturation in the adult, especially of biochemical functions.

BIOCHEMICAL EVIDENCE FOR POSTEMERGENCE MATURATION OF FLIGHT ABILITY

In a study of the relationship between cell number and cholinesterase activity in the brain of the adult worker honey bee, *Apis mellifera* Linnaeus, from emergence to old age, Rockstein (1950) found that the enzyme activity in the whole brain increased by about 15 percent during the first week to 10 days of adult life; this level of activity remained undiminished throughout the remainder of the bee's life. (This was especially significant because the number of brain cells actually fell rapidly during the first 2 weeks of life and then more slowly thereafter throughout adult life; see figs. 1 and 2). The fact that the adult worker bee does not normally make its flights into the field until some time after the first week of life suggested a possible relationship between the parallel biochemical changes and the developing function of flight during this period. Dr. A. G. Richards (1948, personal communication) suggested that the decline in cell content during a time when the enzyme activity was rising, implied a continuing neural maturation extending into the imaginal stage, which includes a biochemical phase as well as the continuation of the loss of larval neurones (into adult life) which was initiated in the pupa. Babers and Pratt (1950), in an attempt to explain conflicting reports

of the effects of DDT on house fly brain cholinesterase, learned that the age of the fly was an important consideration in such experiments. Thus, the cholinesterase activity more than doubled during the first 24 hours of adult life and remained unchanged thereafter for the next 7 days, as is seen in table 1. The accelerated development of brain cholinesterase in this species (in contrast to the 7-day period of biochemical maturation of brain cholinesterase in the worker honey bee) parallels the equally accelerated development of flight ability in the house fly within 24 hours after adult emergence. This interrelationship of developing motor ability with maturation of maximal brain

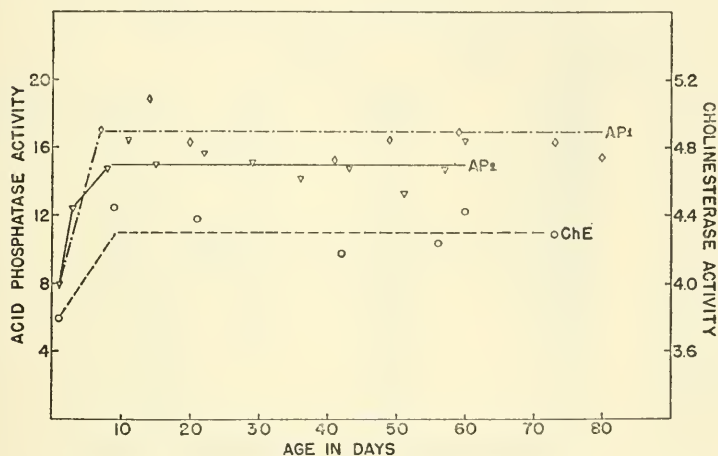


FIG. 1.—Acid phosphatase in whole body and cholinesterase in whole brain homogenates of the adult worker honey bee. (After Rockstein, 1953.)

cholinesterase activity in these two species of insects has its counterpart in several important reports, in which development of motor ability (locomotion) in the embryo and immature young mammals (Nachmansohn, 1939; Sawyer, 1943), as well as the extent of development of locomotor ability in the mature adult of each of two different species of fish, amphibia, and reptiles (Lindeman, 1945), have been related to the cholinesterase content of the brain and spinal cord in these animals. That brain development is characterized by an increase in cholinesterase activity was also demonstrated in the grasshopper *Melanoplus differentialis* by Tahmisian (1943), who observed that such an increase followed secondary differentiation of the neural mass, especially during the formation of ganglia and connectives, in the developing embryo.

Organophosphorous compounds (like adenosine triphosphate) are recognized labile storehouses of relatively large amounts of readily available energy, which is released by the breakdown of such compounds during muscle contraction and in other biological processes like bioluminescence and transmission of certain nerve impulses (Rockstein, 1957). The present writer, therefore, undertook to measure changes in activity of total body acid and alkaline sodium

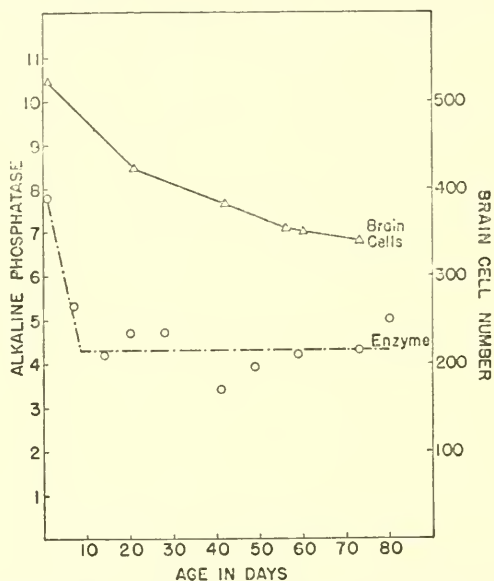


FIG. 2.—Alkaline phosphatase in whole body homogenates and brain cell number in the adult worker honey bee. (After Rockstein, 1953.)

Betaglycerophosphatases in aging adult worker honey bees (Rockstein, 1953). As shown in figure 1, the acid enzyme activity rises rapidly during the early days of imaginal life, so that by the eighth to tenth day the activity is 90 percent higher than that of the newly emerged adult; again this heightened activity remains unchanged throughout the remainder of the bee's life. As shown in figure 2, the alkaline enzyme activity *falls* precipitously during the same period to a level about 44 percent below that found in the newly emerged imago. Thus, just as the brain cholinesterase activity rises during this early phase of postemergent life, the acid enzyme rises in parallel fashion with a reciprocal diminution in the alkaline enzyme content. (Moog, 1946, has stated that the coexistence of these two enzymes in one

organ or tissue signifies a dual, matching dephosphorylating mechanism in the intermediary metabolism of carbohydrates such as glycogen.)

Just prior to the completion of this paper, the writer was particularly gratified to receive from Japan a short report by Sakagami and Maruyama (1956) which stated that the enzyme system primarily concerned with flight muscle contraction (Gilmour, 1953), adenosine triphosphatase (ATPase), extracted from the thoracic flight muscle, showed a similar increase in activity during the first week of adult life in the worker honey bee (fig. 3). The magnesium-activated

TABLE I.—*Cholinesterase activity of normal flies and of those resistant to DDT* *
(After Babers and Pratt, 1950.)

Age (days)	Normal flies		Resistant flies	
	Males	Females	Males	Females
Just emerged	0.187	0.187	0.130	0.142
1	0.475	0.350	0.307	0.212
2	0.437	0.207	0.412	0.187
3	0.545	0.287	0.382	0.187
4	0.512	0.400	0.487	0.200
5	0.612	0.312	0.325	0.207
6	0.427	0.225	0.525	0.482
7	0.645	0.357	0.512	0.350
8	0.502	0.307	0.717	0.337
9	0.262	0.537	0.362
10	0.267	0.255
11	0.317	0.287

* Rates are in milliliters of 0.02 N sodium hydroxide added in 20 minutes.

enzyme especially showed an increase of 100 percent from the 1st to the 5th day and well over 100 percent by the 10th day, with a gradual leveling off in activity thereafter up through the 20th day of adult life. The change in the calcium-activated enzyme followed this pattern precisely, but the increase involved was only about 25 to 30 percent. They also cite the earlier work by Maruyama that ATPase activity rapidly reaches its maximum value in the (shorter-lived) house fly within 1 hour after emergence of the adult from the puparium. This is exciting confirmation of this writer's hypothesis of postemergent biochemical maturation (metachemogenesis) in relation to the development of flight ability; viz, the remarkable coincidence of rise in the brain enzyme related to nerve impulse transmittance and in tissue enzymes related to the energizing of contraction of (flight) muscles in two species of insects from two widely different orders and with two considerably different life spans. These two

Japanese workers also suggest that the discrepancy in such imaginal postemergence maturation times for these two species is related to the solitary existence of the house fly which demands rapid completion of development for survival; the honey bee on the other hand appears to have a somewhat retarded postemergence maturation of this function, in accordance with its social habits and its confinement to the hive for some days after its appearance as an adult. In *Drosophila funebris*

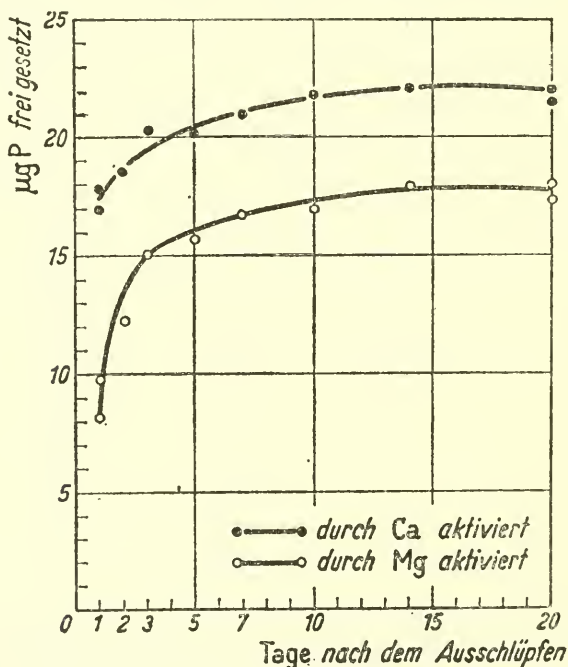


FIG. 3.—Activity of muscle ATPase in the adult worker honey bee.
(After Sakagami and Maruyama, 1956.)

(Fabricius), Williams et al. (1943) reported that the body glycogen more than doubled during the first 3 days and continued to rise to a maximum by the sixth day, after which there was no change from the maximum through the second week (see table 2). Figures 4 and 5 show that these changes in glycogen content followed in parallel fashion the flies' flight ability (as it could be measured in terms of wing-beat frequency or average duration of flight). In a histological-histochemical study of the reserve substances of flight in *Drosophila* sp., Wigglesworth (1949) observed that the larval fat body, rich in fat and protein reserves, persists in the body of the emerged fly; at the

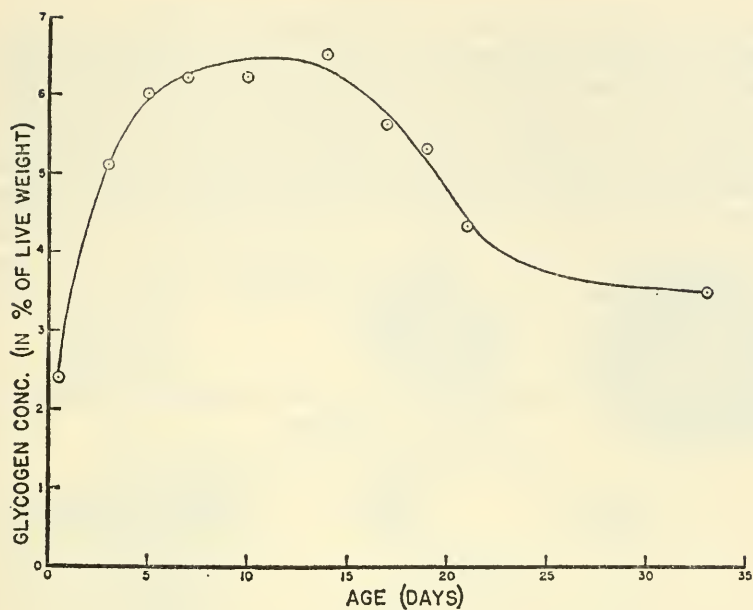


FIG. 4.—Changes in the glycogen concentration of *Drosophila* as a function of the animals' adult age. (After Williams et al., 1943.)

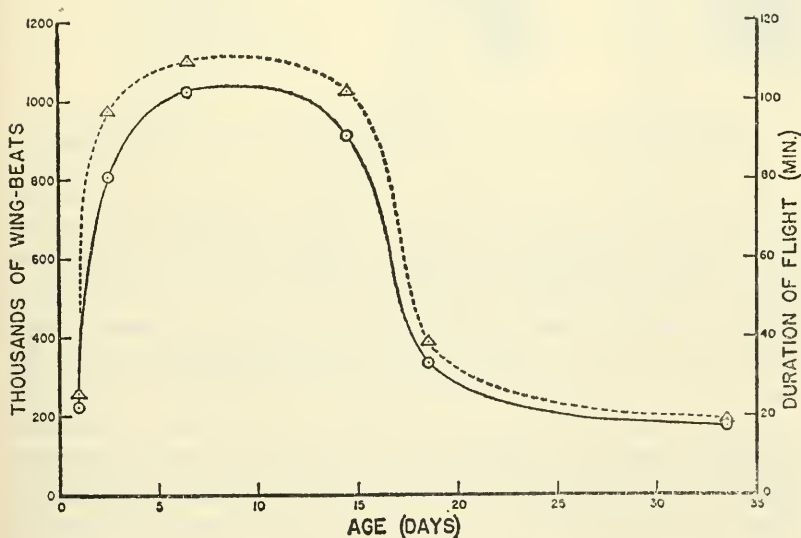


FIG. 5.—The relation between the flight ability and the age of *Drosophila*. Upper curve, average duration of flight as a function of age. Lower curve, average total number of wing beats as a function of age. (After Williams et al., 1943.)

same time the imaginal fat body is reduced in size (fig. 6). During the next 72 hours, the cells of the larval fat body diminish steadily in size and in fat and protein content, while the adult fat body is concomitantly enlarging with the deposition of large amounts of glycogen, especially, to a maximum on this third day, at the end of which the larval fat body cells have disappeared. This mature histological picture of the fat body does not change for 4 to 5 weeks after emergence. Thus, these two reports supply firm histological, biochemical, and functional evidence for maturation of flight ability within a few days after the appearance of the adult fly.

TABLE 2.—*Changes in the glycogen concentration in Drosophila funebris as a function of adult age*

(After Williams et al., 1943.)

Average age (days)	Number of animals	Average concentration of glycogen (in percent of live weight)
0.5	91	2.4
3	72	5.1
5	114	6.0
7	65	6.2
10	77	6.2
14	85	6.5
17	75	5.6
19	31	5.3
21	21	4.3
33	23	3.5

CYTOCHROME OXIDASE ACTIVITY IN THE YOUNG IMAGO

Early studies of the physiology of metamorphosis were concerned with the typical, U-shaped curve for oxygen consumption during the pupal stage of holometabolous insects; but this index of metabolism was not followed into the adult stage. With the recent increased interest in insect biochemistry, the cytochrome system has been studied by Sacktor (1951) in the house fly. (The components of this system mediate electronic transfer from metabolic intermediates ultimately to oxygen and therefore effect the final steps of aerobic oxidation. As such, a knowledge of the details of their changes during metamorphosis would pinpoint the controlling basic respiratory processes involved.) He found that cytochrome *c* oxidase activity followed a typical U-shaped curve during pupal development (for both normal and DDT-resistant strains). Furthermore, in following this activity into adult life (1950), he found that the enzyme activity continued its

ascending tendency by increasing by over 50 percent from 30 minutes to 2 hours of age and by 100 to 200 percent by the third day (figs. 7 and 8). Bodenstein and Sacktor (1952) found a similar U-shaped curve during pupal development of *Drosophila virilis* Sturtevant, for cytochrome *c* oxidase activity, which continued well into the adult stage, with the enzyme activity at emergence equal to that at the beginning of pupation. After emergence the enzyme continued to

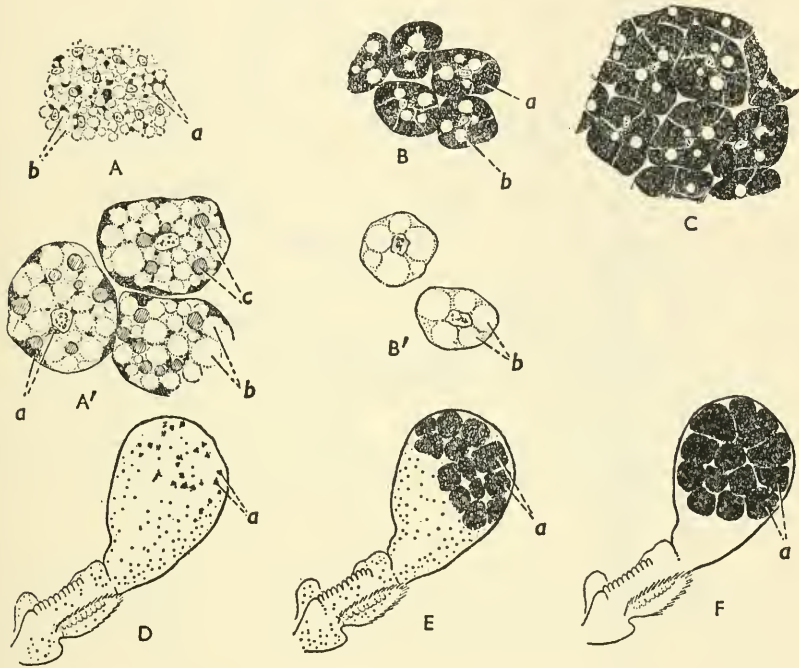


FIG. 6.—Accumulation of glycogen in fat body and halteres in the young fly. A, Imaginal fat body of newly emerged fly. A', larval fat body of the same. B, Imaginal fat body at 48 hours. B', Larval fat body of the same. C, Imaginal fat body at 4 days. D, Haltere of newly emerged fly. E, Haltere at 48 hours. F, Haltere at 4 days, showing progressive increase in glycogen. a, Glycogen; b, fat; c, protein spheres. (After Wigglesworth, 1950.)

increase to a maximum at the end of the third day (see fig. 9), equal to double the activity of the newly emerged imago. It is interesting that Keilin (1925), in his identification of cytochrome in a variety of animals, recognized that its presence in insect flight muscles might be related to their ability to contract at high rates; more important to this discussion, he found that the cytochrome content of newly-formed adult thoracic flight muscles increases during pupal development, and

does not reach a maximum "immediately after hatching," but rather at some time considerably past emergence of the adult insect.

Allen and Richards (1954) have added further evidence for the existence of metachemogenesis in adult *Sarcophaga bullata* Parker, in the form of variation with age of the enzyme system important in the oxidation of succinic acid (an important metabolic intermediate



FIG. 7.—Changes in cytochrome oxidase activity with age of male flies. (• resistant strain; ° normal strain.) (After Sacktor, 1950.)

of the tricarboxylic acid cycle), and the aerobic oxidation of which is effected through the cytochrome system. They found a systematic increase in such oxidative activity by homogenates of the thoracic flight muscles, so that it was double by the third day and triple in value by the fifth to sixth day; this was followed by a gradual, slow rise to a maximum on the ninth day.

INTRACELLULAR LOCALIZATION OF METACHEMOGENESIS

With the appearance of the important work of Watanabe and Williams (1951), the identity of the interfibrillar sarcosomes from the flight muscles of Diptera and Hymenoptera was established as organized units of respiratory metabolism, giant mitochondria. Later,



FIG. 8.—Changes in cytochrome oxidase activity with age of female flies. (• resistant strain; ° normal strain.) (After Sacktor, 1950.)

Levenbook and Williams (1956) found that the mean diameter of such sarcosomes in the flight muscles of *Phormia regina* (Meigen) rapidly increases from 1 to 2.5 micra during the first 7 days of adult life, without any change in mitochondrial number. Concomitantly, the dry weight follows this pattern exactly to reach a value three times higher by the sixth day of imaginal life (fig. 10), just as the cytochrome *c* titer increases to more than threefold during the same period

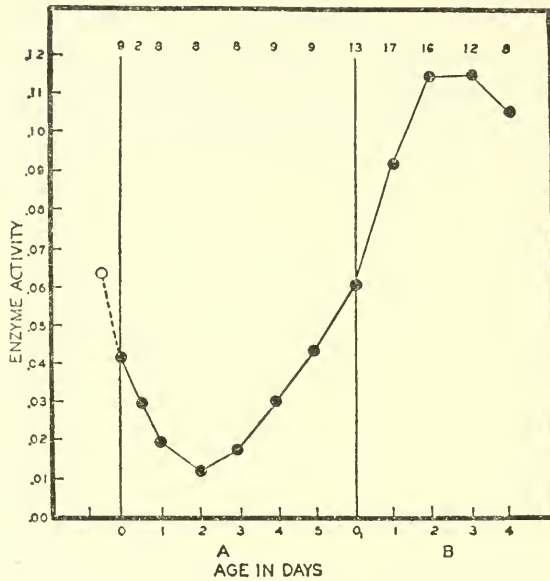


FIG. 9.—Cytochrome *c* oxidase activity of *Drosophila virilis* during the pupal period and the first 4 days of adult life. Abscissa: A, pupal period; B, adult period; O, puparium formation; O₁, emergence of fly. Ordinate: cytochrome *c* oxidase activity. Numbers above indicate numbers of pairs used for the determination of each age group. (After Bodenstern and Sacktor, 1952.)

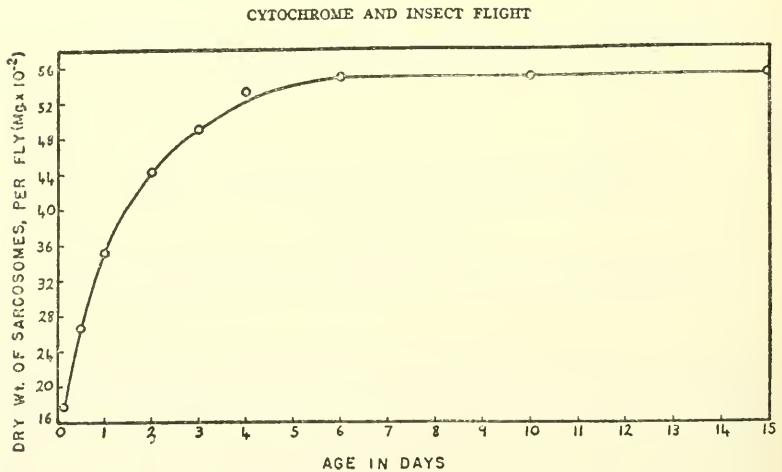


FIG. 10.—The dry weight of *Phormia* sarcosomes as a function of fly age. (After Levenbook and Williams, 1956.)

(fig. 11); finally, the flight ability (as measured by wing-beat frequency) increases sharply to a maximum at 6 to 7 days (fig. 12). Those maximal values all clearly remain unchanged at this mature maximal level for at least 7 days more. In *Drosophila funebris* (Fabricius), Watanabe and Williams (1953) found a similar increase

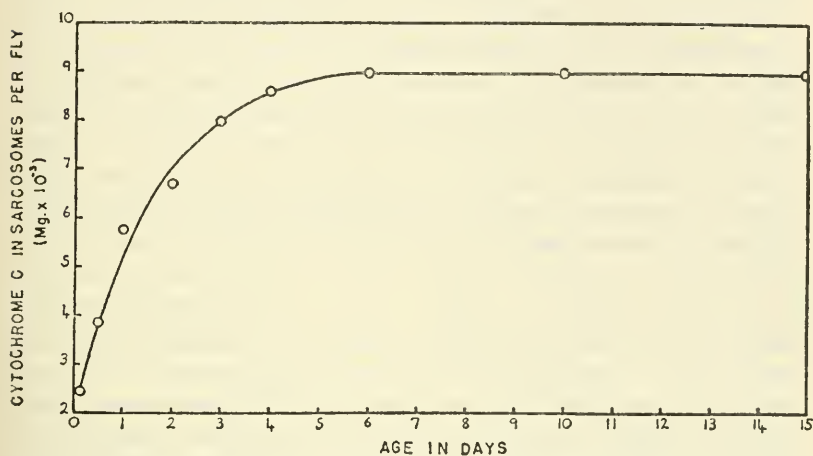


FIG. 11.—Cytochrome *c* titer of isolated *Phormia* sarcosomes as a function of fly age. (After Levenbook and Williams, 1956.)

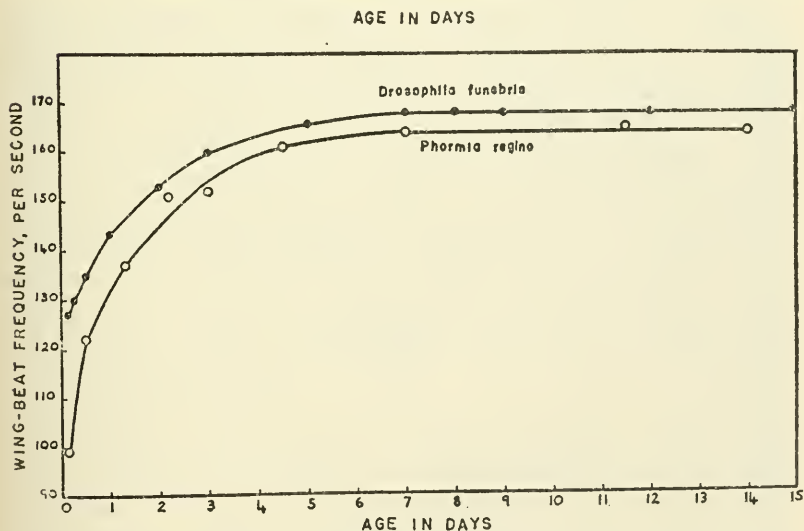


FIG. 12.—Wing-beat frequency of *Drosophila funebris* (from unpublished data of Chadwick and Williams) and of *Phormia* as a function of fly age. (After Levenbook and Williams, 1956.)

in mean diameter by two and one-half times during the first 7 days of adult life; as can also be seen in figure 12 the wing-beat frequency of *D. funebris* (as an index of flight ability) parallels these data for change in sarcosome size in the same species. Thus for two different dipteran species there is strong correlative evidence from several lines of investigation for postemergence maturation at the subcellular level.

As part of a recent study of the respiratory metabolism of fly sarcosomes British biochemists Lewis and Slater (1954) reported that the phosphorylation (P:O) ratio was considerably lower in the sarcosomes of younger than in those of older blow flies, *Calliphora erythrocephala* (Meigen), so that by the 10th day this P:O, as well as the P:alpha-ketoglutarate ratio, was twice as great as that of the young imago. Furthermore, oxidation of alpha-ketoglutarate by such particles isolated in versene was at least doubled by the addition of dinitrophenol (to an incubation mixture which included also glucose and hexokinase) for flies 1 to 2 days of age; no such activation was possible for sarcosomes isolated from flies 9 days of age (Slater and Lewis, 1954). These isolated data represent fragments of a still poorly understood pattern of metachemogenesis within the sarcosomes, which may be eventually linked more precisely with the postemergence maturation of dipteran flight muscle and of the function of flight itself.

EVIDENCE FROM INSECT ENDOCRINOLOGY

Shortly after the appearance of a preliminary treatment of this subject of metachemogenesis as a cryptic, biochemical manifestation of postemergence maturation in holometabolous insects (Rockstein, 1956), the writer received a communication containing several pertinent, stimulating observations from Dr. Berta Scharrer, one of our leading endocrinologists, in which she volunteered additional instances of postemergence maturation in the corpus allatum of such insects. This organ has been the object of intensified study during the past 10 years as the gland that maintains the juvenile state by the secretion of the "juvenile hormone"; conversely, when this secretion ceases "metamorphosis" takes place (Wigglesworth, 1954, p. 94) under the stimulus of the prothoracic (or "thoracic") glands' growth and moulting hormone; (after emergence of the adult the one recognized function of the corpus allatum has been the maturation of the ovaries). Aside from controlling maturation of reproductive function, there is some evidence that the histological changes reported as continuing into adult life may be related to functions other than sexual maturation. Thus, Day (1943) found a persistence of the larval fat body

for 3 days after emergence, during which period its degeneration was paralleled by the increase in size of the adult fat body of *Sarcophaga securifera* Villeneuve; Evans (1935) had made similar observations for the larval and imaginal fat body of *Lucilia sericata* Meigen. Day also noted that the oenocytes, barely conspicuous at emergence time, increase in size along with the adult fat body during the early days of adulthood, after which they appear to remain histologically and histochemically unaltered throughout adult life. Day demonstrated the dependence of the adult fat body and oenocytes upon the secretions of the corpora allata for their maturation in both *S. securifera* and *L. sericata* by a series of experiments, as follows: Allatectomy of the newly emerged adult results in the failure of the larval fat body to disappear and of the imaginal fat body and oenocytes to develop. Allatectomy of flies even as old as 6 days of age had a regressive effect upon the already formed oenocytes, but not upon the fully formed imaginal fat body.

In a direct study of the corpora allata, Pflugfelder (1948) found that the volume and nuclear number of the corpora allata of the drone, worker, and the queen honey bee, *Apis mellifera* Linnaeus, increased in a geometric progression after each larval moult. With "pupation," these values were halved, but again doubled with adult emergence. After emergence, this increase in volume continued in all three castes, with the worker attaining a considerably higher maximum corpus allatum volume than the queen or the drone. Lukoschus (1956) confirmed these findings in the queen and worker honey bee corpus allatum, but extended the study of these changes well into the imaginal life; for the queen bee he found a doubling of the corpus allatum volume to occur by the end of the second year of adult life; for the worker this volume was increased five times within 21 days after emergence, at which time its value was about 20 percent higher than the highest volume attained by the average queen at 2 years of age. Pflugfelder inferred, from this observed growth of the adult corpus allatum in general and especially from the considerably higher activity of the corpus allatum of the sexually inactive worker bee, that such maturation of the corpus allatum is not exclusively related to its gonadotrophic effects.

The means by which the corpus allatum produces its effects upon other organs as well as upon the ovaries has been suggested by the studies of Pfeiffer (1945) in a paurometabolous insect and by Thomsen (1950) in *Calliphora erythrocephala*. Their work, as well as that of Day (1943), cited above, clearly suggests that the corpus allatum

has a regulatory influence upon body metabolism in general, possibly by the release of a metabolic hormone which influences the composition of the fat body and oenocytes as well as total body metabolism (as reflected by oxygen uptake of normal and allatectomized animals of either sex).

Bodenstein and Sacktor's study (1952) attempted to show hormonal-enzymatic interrelationships of the (prothoracic gland and) corpus allatum and cytochrome oxidase activity (see fig. 9, above) during the late pupal and early imaginal life of *Drosophila virilis*. Although considerable evidence has been accumulated by a number of endocrinological studies that the corpora allatum is active from the late pupal stage onward in several insect species, there was found no direct relation between rising enzyme activity and the activity of this gland. Thus, allatectomy in animals 3 hours after emergence failed to arrest the usual progress of rapidly rising cytochrome oxidase during the first 3 days of adult life. It is likely that the failure to demonstrate this interrelationship may have arisen from the fact that the corpus allatum actually triggers such enzyme production and release, considerably earlier than the time at which allatectomy was performed, especially inasmuch as the rise in the enzyme activity has already begun on *the second to third day after the pupal stage* (see fig. 9). Although the mediation of the extrinsic control of metamorphosis itself through the associated cytochrome system has been clearly indicated by the integrated studies of Williams and his co-workers (1951) in the developing pupa of *Platysamia cecropia* (Linnaeus), such a relationship has not been studied beyond the immediate end of the pupal stage and the newly emerged adult insect. From the standpoint of postemergence biochemical maturation, it must be to the details of histological and histochemical changes in the known components of the insect endocrine system that we must intensify our attention, in order to pinpoint the higher levels which control the enzymes and related biochemical components of the uncompleted target organs of the still immature imago.

METACHEMOGENESIS IN HEMIMETABOLOUS INSECTS

Poyarkoff's principal conclusion concerning the nature of the pupa of holometabolous insects that it corresponded to the last nymphal instar of hemimetabolous species was based on a considerable body of evidence, chiefly from comparative morphology. If this concept of the pupa as a preimaginal form similar to the last nymphal instar of the Hemimetabola or more so to the subimago of the Ephemera is

valid, it would be reasonable to expect to find a counterpart of meta-chemogenesis (as it has been described for a number of holometabolous forms) in insect species with such "gradual metamorphosis." At least two such studies have indicated that such a period of post-emergence biochemical maturation may indeed be characteristic of Hemimetabola, as well. Thus McShan and his coworkers (1954) found that succinoxidase activity of the pink thoracic muscles of the Madeira roach, *Leucophaea maderae*, increases significantly from one-half hour of age to the fifth day after the final moult. This elevated activity persists through the 30th day, after which there is another rise in enzyme activity to a maximum at 40 days of adult life equal to 50 percent higher than that of the original half-hour-old adult. In a later study, Kramer and McShan (personal communication, 1955) found that succinoxidase activity of the basal leg-thoracic muscles of the male American cockroach, *Periplaneta americana* (Linnaeus), increased by about 60 percent from the 12-hour- to the 10-day-old adult. In both species, also, they found a slow, continuous increase in dry weight of thoracic muscle over the first 60 days and 10 days of adult life, respectively. Brooks (1957) clarified further the age-succinoxidase activity relationship in the American cockroach; she observed that the biochemical maturation of the pigmented (pink) leg and wing muscles, in terms of succinoxidase activity, has its anatomical counterpart in the degree of pigmentation of the muscles. Thus, in the nymphs of both sexes, all leg and wing muscles are white and the succinoxidase activity is at a minimum. In the male cockroach, the final moult is marked by a rapid increase in pigmentation, accompanied by a concomitant rise in succinoxidase activity in the muscles which are primarily concerned with flight. By the third week of adult life, this activity has reached a (maximum) value equal to about six times that of the newly emerged adult male; this high level is maintained for a considerable period of time thereafter. In the female cockroach, on the other hand, both pigmentation and associated succinoxidase activity do not change for at least 2 months after adult emergence; at this late time (when the male muscle pigmentation and enzyme activity have been at a maximum level for well over a month), the muscles of the female show only a faint pigmentation and possess a succinoxidase activity about one and one-half times that of the younger females and less than one-third that of corresponding muscles from males of the same age.

Finally, as in the case of the Holometabola, endocrinological studies suggest the role of the maturing corpora allata as a higher level con-

trol of biochemical maturation in the Hemimetabola also. Mendes (1948), by a thorough histological study of the corpora allata of both sexes of *Melanoplus differentialis* (Thomas), during nymphal development and adult maturation, has established a positive relationship between changes in these endocrine glands (in the form of the mitotic activity of its undifferentiated cells and characteristic alterations in cell volume and acidophilic granule content of its secretory cells) and nymphal development. At emergence of the adult, such activity of the corpus allatum practically ceases; in the adult female, thereafter the maturation of the ovaries is accompanied by the rapid increase in the activity of the corpus allatum to a maximum level by the end of the second week after the final moult. It is of considerable interest that the male corpus allatum also attains full secretory activity at the same age as the female. In the latter connection, Pfeiffer's work (1945) has demonstrated (for hemimetabolous forms) that the developing corpus allatum of the adult (female) *M. differentialis* may exert a generalized regulatory influence upon body metabolism through the secretion of a metabolic (as well as a gonadotrophic) hormone (just as Day, 1943, showed this to be true in two holometabolous, dipteran species).

THE INEQUVALENCE OF THE MOMENT OF EMERGENCE

That the extent of adult differentiation at the time of emergence is different for different species of insects (Scharrer, personal communication, 1956) is indicated strongly by the numerous data presented above. In the case of two species of hemimetabolous insects mentioned, the succinoxidase activity and dry weight of the pigmented thoracic muscles related to flight reach a maximum level at some time between 30 and 40 days in the Madeira roach, but at only 10 days of adult age in the male American cockroach. These muscles, in the case of the female American cockroach, on the other hand, take about 2 months to reach a maximum succinoxidase content. In the Holometabola, maturation of flight ability, in terms of maximum brain cholinesterase activity, maximum body acid phosphatase (and concomitant minimum alkaline phosphatase) activity, maximum adenosinetriphosphatase activity of the thoracic flight muscles, and observed flying ability all occur within 7 to 10 days after adult emergence in the case of the worker honey bee. In the house fly, maximum levels of brain cholinesterase, body cytochrome *c* oxidase, thoracic muscle adenosinetriphosphatase, and the ability to fly are all reached at about the second day. In *Drosophila* spp. the glycogen content, cytochrome *c*

oxidase activity, size of thoracic muscle sarcosomes and flight ability (as measured in terms of duration of flight and wing-beat frequency) all become maximal by the sixth day of adult life. In the blow fly, *Phormia regina*, the size, dry weight and cytochrome *c* titer of such sarcosomes, as well as wing-beat frequency reach maximum levels on the seventh day after adult appearance.

In the matter of degree of development of endocrine function at adult emergence, Scharrer (personal communication, 1956) has pointed out that the corpus allatum, especially, shows considerable variation in extent of maturation, from species to species, at the "moment of emergence." In addition to the fairly extensive literature linking maturation of the ovaries of adult insects to corresponding development of the corpora allata (Pfeiffer, 1945, Thomsen, 1950, and Wigglesworth, 1954), evidence has been cited above for variation in time of completion of maturation of the corpora allata of different species and even between sexes in one species in relation to other body functions, like fat body and oenocyte development and total body metabolism. This seems to be true for the prothoracic glands of different species, as well. Thus, this gland (or its homologous structure), which secretes (the moulting and) the growth and differentiation hormone, disappears within 24 hours after "metamorphosis" in the bug *Rhodnius*, whereas in *Periplaneta americana* the prothoracic glands persist for at least 2 weeks after the final moult.

A recapitulation of the numerous data and observations presented above indicates that there indeed exists a continuity from the juvenile stages into the adult stadium in holometabolous as well as hemimetabolous insects, which is especially evident in the continuation of biochemical maturation for a considerable time after the last moult. This period of metachemogenesis can only be reflective of maturing adult functions, which are incompletely developed at the time of adult emergence in the case of Holometabola (to a greater or less degree in different species of insects).

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A PHYSIOLOGICAL APPROACH TO THE RELATION BETWEEN PREY AND PREDATOR¹

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(WITH 5 PLATES)

BEHAVIOR AND EVOLUTION

The description of animal behavior in terms of its underlying neuronal organization preoccupies an increasing number of workers. Human egocentricity naturally dictates that much of this work be done on the higher vertebrates, but the extreme complexity of the problem at this level has so far limited tangible results to the simplest reflexes. Difficulties are due not only to the size of the neuron population which mediates behavior in the higher animals, but also to the increasing plasticity of their behavior.

The student of behavior mechanisms faces problems whose general nature is surprisingly like those encountered in searching for the organic basis of evolution. In a stimulating essay Pringle (1951) points out the analogy between the evolution of a species through selection and the appearance of behavior patterns in an individual animal through learning. In the course both of evolution and of learning the trend is toward complexity and organization and away from randomness. In the evolution of body form the increase in complexity is structural, while in learning the complexity has a temporal dimension. Species within a genus or genera within a family differ in appearance by a number of modifications of recent acquisition and have in common, as a group characteristic, a relatively immutable core of more anciently acquired body organization. Similarly, individuals of a species may differ from each other in their behavior by response patterns learned during their respective lifetimes but they still share a core of innate drives or instincts characteristic of the species and ancestral in origin. To extend the comparison further it could be pointed out

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that systematics and genetics, the descriptive and experimental sciences of evolution, have their counterparts in ethology and neurophysiology which are concerned respectively with the description of animal behavior and its functional basis.

The comparison made by Pringle appears to be no more than a striking analogy, there being no obvious causal relation between racial modifiability and individual learning capacity. For instance, the class Insecta shows intense adaptive radiation, variety of form, habit, and habitat being associated with a wide range and complexity of innate behavioral patterns. However, the ability of insects to learn is not generally marked except for some notable examples among the Hymenoptera which are then possible only under relatively stereotyped circumstances. It could be argued that the ability to learn has little survival value when compared with a set of complex "built-in" reactions in an animal as short-lived as are most insects, but it seems worthwhile to consider this question from a neurophysiological angle.

Although we still lack any real knowledge of the organic basis of learning, it would seem that the capacity of an individual to form novel combinations of stimulus patterns with effector patterns must depend upon the capacity for a very great number of potential combinations or interactions between central nervous units. The number of these interactions which is theoretically possible must depend in some degree upon the actual number of central nervous units or neurons available for combination. It seems unlikely that any organism learns to its full capabilities during its lifetime, thereby realizing all potential combinations. However, there must be a great superfluity of nervous units in organisms having a greater learning potential.

Conversely, if the number of neurons in the nervous system is strictly limited one might expect behavior to be predominated by innate or instinctive patterns. In this case the necessary neuron combinations would be determined phyletically like body form and need involve no superfluity of nerve units. Since the general behavior of insects falls into this pattern I suggest that an economy or parsimony of nerve units is an important factor in the organization and operation of their nervous systems. In the following pages I shall examine the possible basis of this neural parsimony in relation to neural mechanisms of obvious survival value—predator evasion and predation.

THE PREY

Speed of operation must be a prime requisite in the neural mechanisms by which insects detect and evade predators. It seems reasonable to suppose that speed would dictate simplicity of mechanism, as

in man-made alarm systems, and that analysis of evasion systems might be likely to lead to a more complete picture of the neural basis of behavior of obvious survival value. The physiology of three evasion systems in insects has been partially explored. Although our information about them is still most inadequate, they will serve as a basis for the present discussion.

The abdominal nerve cord of the cockroach, *Periplaneta americana*, contains several so-called giant fibers which occupy about 12 percent of its cross-sectional area (Roeder, 1948). The largest of these fibers is about 30 microns in diameter, exceeding in this respect the largest (alpha) nerve fibers in the mammalian nervous system. In addition to the giants the nerve cord shows a relation of fiber diameter to frequency which is not dissimilar to that found in vertebrates (pl. 1), and it must be concluded that the total number of fibers in the cockroach nerve cord is much less. The giant fibers, which take up so much space in proportion to their number, are the internuncial units in an alarm reaction (Pumphrey and Rawdon-Smith, 1937; Roeder, 1948) which will be discussed below. A second example of a small number of units participating in an alarm reaction and at the same time performing more complex tasks is to be found in the jumping muscle of the locust. Hoyle (1955a) has shown that the largest muscle in the body of *Locusta migratoria*, the extensor tibiae of the metathoracic leg, is supplied by three motor nerve fibers, only two of which have a clear motor function. A third example, this time of a sensory nerve, is provided by the auditory organ which enables certain families of moths to detect the approach of predatory bats (pl. 2, fig. 1). It contains only two acoustic receptor cells (Eggers, 1938) and one accessory cell of undetermined function (Roeder and Treat, 1957). Analogous mechanisms in vertebrates involve thousands of separate nerve fibers.

In order to appreciate the relative merits of nerve systems composed of a few large units versus those composed of many small units we must consider the factors affecting impulse transmission in a single nerve fiber. A single axon, however large, can convey only a limited amount of information from one point to another because of the on-off or all-or-none nature of the nerve impulse. Therefore, several small fibers are able to convey a much greater range of information than a single large fiber simply because with several units the coding possibilities are greater. To offset this disadvantage the single large fiber conveys its information more rapidly, the velocity of impulse conduction being roughly proportional to fiber diameter. Since the three systems mentioned above are all involved in the detection of, and

escape from, predators it is obvious that in these cases a short reaction time has much greater survival value than detailed information. A millisecond or so within the nervous system must often mark the difference between the quick and the dead.

The adaptive value of speed at the expense of detail in such alarm and escape systems cannot be questioned, but one may well ask why large fibers, such as those in the cockroach nerve cord, occupy such a disproportionate amount of central nervous space when compared with analogous alarm systems in vertebrates. All vertebrate nerve fibers capable of high-speed impulse conduction are surrounded by thick segments of myelin interrupted at regular intervals by nodes of Ranvier. In insects the lipid material surrounding the largest axons is so thin that it can be detected only by special staining and optical techniques. Myelination, for reasons which will not be debated here, appears to improve conduction velocity about tenfold when fibers of similar diameter are compared. For instance, at room temperature locust motor fibers 10 to 13 microns in diameter conduct at 2.2 meters per second (Hoyle, 1955a), cockroach giant fibers of 30 to 40 microns conduct at 6 to 7 meters per second (Roeder, 1948), while myelinated frog axons only 7.5 microns in diameter conduct at 25 meters per second (Taylor, 1942). For some reason myelination has never appeared in insects. Hence, their simple but vital alarm systems must occupy a large amount of space in their nervous systems if reaction times comparable to those of vertebrate predators are to be achieved. Quality of information is sacrificed to speed, which implies a limitation or economy in the number of nerve units unless the central nervous system is to occupy a disproportionate amount of space in an organism which for other reasons appears to be limited in total body size.

This parsimony of neurons makes insects excellent subjects for that branch of neurophysiology which seeks to provide a neural basis for behavior. The presence of a smaller number of units implies that the central nervous system must be a simpler communications network compared with that of vertebrates and therefore more susceptible to eventual analysis, even though at the same time it is obviously an effective system for integrating nerve activity into behavior of some complexity and variety. Other technical advantages of insects for this sort of work are the accessibility of the nervous system, its division into anatomically distinct and partially autonomous ganglia, and the ease of maintaining ganglion function without special perfusion. But let us turn to the question of the transmission of information in systems containing a minimum of separate pathways.

The simplest form into which a change in the external world can be coded by a sense organ is a single propagated impulse in one nerve fiber. Such information reaching the nervous system could initiate only an all-or-nothing response just as the sounding of the alarm in the station house can initiate only a maximum effort in the fireman irrespective of the size of the fire. While this condition may be approached in some of the alarm systems of insects, most sense organs, even those composed of one or a few units, are able to transmit to the nervous system some impulse-coded information on stimulus intensity, form in time or space, and quality.

This principle is illustrated here by electrical recordings of nerve impulses in the tympanic nerve of a noctuid moth, *Prodenia eridania*. When the ear is exposed to a continuous pure tone (pl. 2, fig. 2) the most sensitive of the 2 acoustic sensilla responds with a short burst of impulses due to the abrupt onset of the tone or switching transient. It then continues to fire with a falling frequency which depends upon the intensity of the tone. At a sound intensity of 23 decibels above that producing the threshold response the second less sensitive sensillum adds its electrical response to complicate the record. If the sound is a very brief click (pl. 3, fig. 1) its intensity is represented in the nerve response by the number of impulses in the after-discharge, which may continue for 10 to 12 milliseconds after the cessation of the stimulus, and by the response of one or of both acoustic units.

A third temporal dimension of the response which varies with stimulus intensity is the latency. This interval between stimulus and response becomes shorter at higher sound intensities, decreasing by about 2 milliseconds between A and D in plate 3, figure 1.

In this simple system the dimension of intensity in the external change is coded as a dimension in time (duration, latency, or frequency of discharge), the form in which information is most frequently dealt with by the nervous system. If the population of sense cells consists of two or more with differing thresholds the stimulus intensity could be centrally represented in a spatial form as well, when discrimination of stimulus quality and direction also becomes possible. By observing on the oscilloscope the response patterns and the relative latencies recorded simultaneously from the right and left ears of a moth exposed to a movable source of clicks it is quite possible to tell whether the source is located on the right or left sides or in the median plane of the moth (Treat and Roeder, unpublished). The most obvious difference between responses of the two ears (pl. 3, fig. 2) is the shortening of the latency on the side receiving the

stronger stimulus. Since the tympanic membranes are about 0.5 cm. apart only a small fraction (about 0.02 msec.) of this latency difference could be due to the difference in the length of the path traveled by the sound, most of it being due to the longer time taken by a weaker stimulus to set off a propagated impulse in the sense cell (compare with pl. 3, fig. 1). Thus, the moth appears to have an effective means of determining the approximate direction (right or left) of a sound source, although there is as yet no behavioral evidence that the intact insect is able to act upon this directional information gathered by its auditory organs.

The sensory characteristics and the behavioral significance of the noctuid ear have been discussed elsewhere (Roeder and Treat, 1957) and will be mentioned only briefly. Electrical recording from the tympanic nerves reveals that noctuids are capable of hearing sounds ranging from 3 kilocycles to well over 100 kilocycles per second, although there is no evidence that one pitch can be discriminated from another. A comparison of plate 2, figure 2, and plate 3, figure 1, suggests that the ear is much more efficient in translating sound into nerve impulses when the sound is chopped into a series of short bursts or pulses; for instance, during a steady tone the impulse frequency declines owing to sensory adaptation while the effects of a brief pulse can be said to be amplified by the presence of the after-discharge. This characteristic enables the noctuid ear to follow the rapid succession of ultrasonic pulses emitted by an echo-locating bat (pl. 4, fig. 1), and the resulting changes in flight pattern (Treat, 1955) are of undoubted survival value to the hunted moth. Although other behavioral functions are suggested by the observation (Roeder and Treat, 1957) that the ear can detect short sound pulses emitted at wing-beat frequency by another moth in flight, as well as by the rough directional property mentioned above, the extremely small number of sensory units suggests that certain other sensory refinements have been sacrificed to speed and certainty of operation—prime characteristics in the detection of an active predator.

Since the central nervous system converts stimulus dimensions into time sequences, the latter must be decoded at the motor end and converted once more into the physical magnitudes of muscle tension or limb displacement. This is shown very beautifully in insects because of the small number of nerve fibers in their neuromuscular systems. Thanks to the fine work of Hoyle (1955b) we have a fairly clear picture of the operation of the jumping muscle of the locust mentioned above. This large muscle can catapult a locust weighing 1.5 g.

in a trajectory 30 cm. high and 70 cm. long, wherefore it develops the astonishing tension of 20,000 g. per g. of muscle. At other times it develops quite gradual and gentle contractions while participating in walking and running. In vertebrates a similar range of tensions in a comparable muscle, such as the gastrocnemius, depends upon the presence of several hundred motor nerve fibers each supplying a small group of muscle fibers. Graded tensions are produced when varying numbers of these motor units are excited in the central nervous system. However, the locust extensor tibiae is supplied with three motor fibers, only two of which appear to be directly excitatory to the muscle fibers. The fast or F fiber innervates all the muscle fibers and produces a near-maximal twitch when an impulse passes along it. A short burst of impulses produces a slightly higher tension, but in any case the locust can only jump when the F fiber is excited, and the F system is clearly concerned with the all-out effort of escape. The slow or S_1 nerve fiber innervates only 30 percent of the muscle fibers, and single impulses in it fail to produce any significant degree of muscle shortening. However, the S_1 fiber operates through temporal summation—the reciprocal of the intensity to frequency coding encountered in sense organs. Thus, 10 impulses per second in the S_1 fiber cause a smooth, gradual tension to develop in the muscle. Further increases in impulse frequency cause corresponding smooth increases in muscle tension, which becomes maximal at about one-quarter of the F-generated tension when 150 impulses per second are passing down the S_1 fiber. Combinations of activity in F and S_1 seem able in this way to provide the wide range of tensions and speeds encountered when this muscle participates in predator evasion and normal walking.

From this brief discussion it seems clear that the great survival value of speed to the prey and the inherently slow conduction in insect nerves have played a part in reducing the number of nerve units concerned in a startle reaction to an extreme minimum. Although much discriminatory capacity is thereby sacrificed, a considerable amount of information can still be coded by the two-unit systems of the moth and locust.

Conduction along nerve fibers consumes only part of the time required for an animal to respond to a stimulus. The rest is taken up by synaptic and neuromuscular delays, temporal summation at synapses, and possibly by hitherto unrecognized neural phenomena. It may well be asked if that fraction of the response time occupied by impulse conduction is sufficiently large so that differences in conduction velocity could alter the startle response time to a significant

extent. The level of significance in terms of predator evasion and racial advantage is impossible to assess. However, some light on the matter may come from measurements of the startle response time and determination of that fraction of it which is occupied by nerve impulse conduction.

THE STARTLE RESPONSE TIME

The competition between prey and predator is the oldest game in the world. It must be the prototype of most man-made contests for two, and like them contains a reasonable chance for either competitor—an inevitable condition if both races are to survive. Unfortunately there appears to be no available analysis of the odds and hazards to each party in any prey-predator contest, but a significant factor in this contest must surely be the strike time of the predator and the startle time of the prey. Further, the selective advantage of a short time to both parties might be expected to reduce these time intervals to a minimum value which would be similar in both cases. Since the predator in one contest is often the prey in another the strike and startle times in widely differing animal groups might affect each other, and hence might reach similar minimum values. It is admitted that the singling out of a single factor such as reaction time from a complex and little understood relationship is a highly questionable procedure. Many other factors, such as relative numbers of prey and predator, must play a major part in balancing the contest. Nevertheless, it provides an excuse for considering data on startle response times in insects.

Such data are scarce, and there does not appear to be any available in relation to a specific predator. Treat (1955, 1956) used a kymographic method to register the interval between the onset of an ultrasonic stimulus and the change in flight pattern shown by various noctuid moths. Tests on 14 females and 27 males of *Graphiphora c-nigrum* L. gave a range of startle times of 75 to 262 msec. (milliseconds) with an average of 139 msec.

A well-known response in insects which falls into the same category as startle reactions is the tarsal flight reflex (Fraenkel, 1932; Chadwick, 1953) in which movements of the wings follow loss of tarsal contact. In the course of studies of the electrical and mechanical events accompanying excitation of insect flight muscle (Roeder, 1951) the onset of these events was determined oscillographically when a platform was suddenly removed from beneath the tarsi of a suspended insect (pl. 4, fig. 2). A reexamination of the records obtained during

this study yielded the following time intervals between loss of tarsal contact and the onset of active flight movements: *Phormia regina* at 18° to 25° C., 45, 50, 50, 60, and 65 msec; an unidentified tabanid, 55, 65, and 85 msec; *Eristalis* sp., 45, 60, and 65 msec. A few measurements with Hymenoptera gave much more variable flight reflex times, a warmup period being necessary under certain conditions in this order. The shortest time obtained was 70 msec. in an individual honey bee at 25° C. With other bees and with *Polistes* the time was often as long as 300 to 400 msec., and flight could not be initiated at all by this method in many instances.

An attempt was made to measure the startle response time of the cockroach, *Periplaneta americana*. Adult males were used and the experiments were carried out at room temperature. A light wooden support was fixed with wax to the pronotum and inserted into a piezoelectric phonograph pickup. The feet of the insect rested on a freely movable paper platform so that any sudden backward thrust of the legs was registered as a forward thrust by the support and pickup. A second pickup was mounted near the cerci so that it registered the arrival of a puff of air directed at this region. The time interval elapsing between deflection of the second pickup by the air blast and the deflection of the pickup attached to the pronotum was measured by recording the electrical output of both on a cathode-ray oscilloscope.

The insects were restless under this restraint, and chance movements invalidated many of the measurements. Another source of error lay in the uncertainty of what constituted a critical level of stimulus as the air blast grew in intensity. Twenty-three measurements gave an average value of 54 msec. and a range of 28 to 90 msec.

Resolution of the startle response of the cockroach into its constituent neural events was next attempted. Previous studies (Pumphrey and Rawdon-Smith, 1937; Roeder, 1948) have shown that mechanical displacement of lightly balanced hair sensilla on the cerci generate afferent impulses in the cercal nerve fibers. The latter form synapses in the last abdominal ganglion with the giant fiber system mentioned above. The giant fibers ascend the abdominal nerve cord without further synapses although they decrease in diameter and conduction is slowed as they pass through the neuropile of each abdominal ganglion. On reaching the metathoracic ganglion the giant fibers form unstable synapses with the system of motor neurons innervating the metathoracic legs whence they continue up the nerve cord to form similar connections in the prothoracic and mesothoracic ganglia (pl. 5).

Rearward extension of the powerful metathoracic legs is an important component of the startle response pattern. Accordingly, an estimate was made of the minimum number of discrete neural events occurring between deflection of hair sensilla on the cerci and contraction of the extensor tibiae muscle. These are: (1) Excitation of the hair sensilla, (2) impulse conduction in the cercal nerve fibers, (3) transmission across the relatively stable cercal nerve-giant fiber synapses in the last abdominal ganglion, (4) impulse conduction in the giant fibers up the abdominal nerve cord, (5) transmission across unstable synapses between the giants and motor system in the metathoracic ganglion, (6) conduction in the fast motor fibers to the extensor muscles, e.g., in nerve 3B to the extensor tibiae, (7) neuromuscular excitation and muscle membrane depolarization (muscle potential), and (8) development of tension in the muscles.

The times occupied by some of these neural events were measured in the following way. A cockroach was pinned to a cork plate and appropriate regions of the nervous system were exposed by dissection. An abrupt mechanical stimulus was applied to one cercus in the form of an electrically timed blow delivered by a small stylus attached to a loud-speaker element. The resulting movement of the cercus was detected by a transducer, and had an abrupt onset followed by a vibration lasting for several milliseconds (pl. 5, upper trace in A, B, and C). Electrodes were placed at various points on the nerve pathway to determine the time of arrival of nerve impulses elicited by the mechanical stimulus (pl. 5, lower trace in A, B, and C). Measurement of arrival times at certain points were made from a number of records similar to that illustrated. Average values were as follows: The afferent volley arrives at a point midway on the cercal nerve in 1.2 msec., the initial giant fiber volley leaves the last abdominal ganglion 3.4 msec., and enters the metathoracic ganglion 6.2 msec. after the onset of the cercal stimulus. The synaptic delay in the last abdominal ganglion occupies 1.1 to 1.5 msec. (Roeder, 1948, 1953). Subtraction of this delay from the last measurement leaves 4.7 to 5.1 msec. occupied by events 1, 2, and 4—that is, by impulse conduction in the cercal nerves and giant fibers.

The synapses in the metathoracic ganglion (event 5) could not be made to transmit with any reliability under the conditions of this experiment. The reasons for this are discussed below. Therefore, this event was bypassed as unmeasurable, and events 6, 7, and 8 (motor nerve and muscle response) were examined. This was done by applying an electric stimulus to nerve 3B at the point where it leaves the metathoracic ganglion. The arrival at the extensor tibiae of impulses

in this nerve and the muscle response (muscle potential) were detected by electrodes inserted into the muscle through holes in the proximal end of the femur. The contraction of the extensor tibiae was registered by an electromechanical transducer attached to the tibia.

The sequence of events recorded in this way is shown in plate 5. The small deflection on the solid line indicates the moment of stimulation of nerve 3B near the metathoracic ganglion. The small diphasic deflection which follows by about 1.5 msec. indicates the arrival in the muscle of the efferent impulse. This is followed by the large monophasic muscle potential lasting for 3.5 msec. The muscle potential is the sign of membrane depolarization and the spread of excitation over the muscle fibers. As the muscle potential decays, contraction (shown by line broken at 1.0 msec. intervals) begins and reaches a maximum in an additional 4.0 msec.

The duration of these events may be summarized in the following form:

	msec.
1. Excitation time of sensilla—unknown, probably.....	0.5
2. Conduction time in cercal nerve.....	1.5
3. Synaptic delay in last abdominal ganglion.....	1.1–1.5
4. Conduction time in giant fibers.....	2.8
5. Synaptic delay in metathoracic ganglion.....	unknown
6. Conduction time in fast motor fiber of 3B.....	1.5
7. Neuromuscular delay and muscle potential.....	4.0
8. Development of contraction.....	4.0
	<hr/>
Total time less event 5.....	15.8

The total duration of events 1 through 8 is considerably less than the average startle time of 54 msec. as determined in the intact insect. However, this total does not include event 5. The synaptic delay in the metathoracic ganglion is difficult to assess for two reasons. First, it is necessary to place the insect under considerable restraint if electrodes are to be placed under its nerves. It seems probable that this condition produces a state of frequent or continuous "startle" in the insect and causes failure of the rapidly adapting synaptic system in the metathoracic ganglion. Second, in the few cases where volleys in the ascending giant fibers elicited motor discharges from the metathoracic ganglion it was evident that several successive volleys were necessary, that is, that the metathoracic synapses operate through temporal summation (Roeder, 1948). If this is so it becomes impossible to define the synaptic delay, which then depends upon the state of adaptation of the synapse, that is, upon the number of successive

volleys which must sum in order to produce a motor discharge. If it is assumed that the minimum requirement for excitation is two volleys in sequence separated by an interval of 2.0 msec., and that there is a ganglionic delay of 2.0 msec., then 4.0 msec. must be added to the total time as determined above. This total time is approximately 21 msec., an interval not much less than the minimum startle response time of 28 msec. determined in the intact insect.

The variability of the startle response time (28 to 90 msec.) and the rapid decline of the startle response in free roaches exposed to repeated puffs of air can also be ascribed to temporal summation and rapid adaptation in this metathoracic synaptic system. Short response times probably occur when the metathoracic synapses are disadapted and the stimulus is strong, when only a small number of serial volleys are needed to excite. After recent stimulation a longer sequence would be needed to discharge the partially adapted synapses. Other factors, such as the presence of the head ganglia, play a part in transmission at this synaptic system (Roeder, 1948).

Earlier in this discussion it was suggested that conduction velocity in nerve fibers plays a significant part in the effectiveness of predator evasion. In the analysis given above, events 2, 4, and 6 include only simple conduction along axons. The sum of the times occupied by these events is 5.8 msec.—about 10 percent of the average startle response time of 54 msec. If the shortest values of the startle response time are considered, then impulse conduction must occupy more than 20 percent of the total time. It is fruitless to speculate on the actual survival value to an organism of an improvement of 1 or 2 percent in its chances of being able to evade a predator (considered highly significant by Ford, 1957), but it is worthwhile to point out that in the cockroach system this end would be accomplished merely by a 10-percent increase in conduction velocity in the axons concerned in the response without any improvement in other nerve functions. As pointed out earlier, an improvement of this kind seems possible in invertebrates only through an increase in fiber diameter, although in the vertebrates the appearance of a thick myelin sheath has been associated with an increase of several hundred percent in conduction velocity.

Measurements of the startle response time in other animal groups could not be found in the literature, although they probably exist. It is interesting to note that the shortest startle response time in man, that of the eye blink to the sound of a pistol shot, is 20 to 54 msec. (Landis and Hunt, 1938). Other facial responses follow 52 to 140 msec. after the stimulus. These figures fall into the same range as

those obtained for insects, bearing out the possibility that startle response times in animals which are likely to interact or compete tend to reach the same minimum values.

THE PREDATOR

From the foregoing it is concluded that in the startle response of the prey quality of information is subordinated to speed of operation and simplicity of neuronal connections. The information requirements of a predator are much more complex, and will certainly be more difficult to analyze in terms of the essential neural events.

In the case of a predator whose prey are active and able to escape, feeding behavior may be divided roughly into two stages. During the first stage, the stalk, detection, identification, and orientation to the prey require the reception and integration of a considerable amount and variety of information, and speed at this stage may be neither possible nor essential. The second stage, the attack, depends upon speed in those predators whose prey is active, and may be steered entirely by information gathered during the first stage.

An excellent example of this type of behavior is seen in the capture of other insects by the praying mantis. The factors directing the strike of the forelegs in *Parastagmatoptera unipunctata* and other Mantidae have been analyzed in some detail by Mittelstaedt (1954, 1957). The final stage in the attack, extension of the prothoracic legs followed by flexion of the spined tibia on the femur so as to grasp the prey, appears to be so rapid as to be unsteerable during its execution, and is analogous to throwing a ball or firing a gun. According to Mittelstaedt extension of the forelegs is accomplished in 11 to 30 msec.

The full strike up to the instant of contact with the prey takes somewhat longer. This was determined by attaching a balsa wood support to the prothorax of an adult mantis. The support was inserted in a phonograph pickup so that sudden forward acceleration of the prothoracic legs at the beginning of extension produced a ballistic recoil in the mantis and support and a pulse of current in the pickup. The feet of the mantis rested on a light paper platform suspended from a thread and counterbalanced with a weight roughly equivalent to that of the mantis. This method of mounting permits practically normal behavior and prey capture (Mittelstaedt, 1954, 1957). A live fly was attached by wax to a small rod in another pickup and moved within striking distance of the mantis.

When the mantis struck at the fly the recoil of its body triggered

the sweep circuit of a cathode-ray oscilloscope having a long-persistence screen. Contact with the fly generated a pulse in the second pickup which was displayed on the oscilloscope as a vertical deflection. The position of this pulse on the timed sweep was measured directly from the tube face. Owing to caprices of mantis appetite, double strikes, and the general unpredictability of the action, only five clear-cut strike times were obtained from a number of strikes. These were 48, 51, 58, 62, and 75 msec. It is interesting to note that these strike times correspond quite closely to the startle times of potential prey recorded in the previous section.

The complex part of this feeding behavior consists of the operations which steer and release the strike. Mittelstaedt has shown that direction is determined by a combination of visual and proprioceptive information. Upon detection of the prey the mantis turns its head in this direction. When the prey is in any position other than directly in front of the mantis this head movement does not bring the prey completely into the visual fixation line. This happens because increasing asymmetry of the nerve discharge from proprioceptive hairs on the right and left cervical sclerites tends to restore the head to its resting straight-ahead position with respect to the prothorax. This fixation deficit is small but constant, and is proportional to the angle by which the head deviates on the prothorax in turning toward the prey. In a number of ingenious experiments Mittelstaedt (1954, 1957) has shown that movements of the head in following the prey are steered by the difference between the optic center message (the neural equivalent of the slight optic asymmetry expressed by the fixation deficit) and the proprioceptive center message (the neural equivalent of asymmetric stimulation of the neck proprioceptors). At the moment of attack this information determines the direction of the strike.

From this it appears that the stage of taking aim depends upon complex and relatively time-consuming processes. Fine quantitative discrimination from two or more sensory systems must be centrally integrated before the direction of the final attack is determined. The compound eyes of the mantis, the primary sense organ in this operation, consist of many thousands of ommatidia connected to the nervous system by a large number of very short nerve fibers. The complexity of the optic ganglia, to which these fibers pass, has so far prohibited any analysis of the central representation of the visual sense. Similarly, the cervical hair plates each contain several hundred tactile sensilla, and the fibers running from them to the prothoracic ganglion must be of small diameter. The direct tracing of the nerve pathways

concerned in prey location and capture will undoubtedly be a complex undertaking. However, the behavioral studies mentioned above lead to a number of definite postulates which Mittelstaedt is attempting to test by electrophysiological methods. A parallel morphological study of neuron relations in the prothoracic and head ganglia of the mantis is also essential to a coherent picture of the mechanisms of this interesting segment of behavior.

DISCUSSION

The achievement of rapid response times at the expense of much central nervous space occupied by a few giant nerve fibers is common throughout the invertebrates. The well-known giant motor axons of cephalopods provide an example. Giant internuncial fibers mediating the withdrawal reflex in annelids have also been intensively investigated (Bullock, 1948, 1953) and a similar situation exists in the Crustacea (discussed by Wiersma, in press). Thus, some of the neurophysiological experiments related above have been performed on other organisms, and the general significance of giant fiber systems in the avoidance of predators is widely recognized.

In spite of this there have been few attempts to relate neurophysiological information of this kind to the actual performance of adaptively significant behavior in the intact animal. Some large fraction of neurophysiological endeavor is rightly directed to establishing a physico-chemical basis for nerve function, but it seems to me that we now have sufficient information on the behavior of nerve cells (see Eccles, 1957) to justify a more intensive effort to find a neural basis for the behavior of animals. This was probably the original object of nerve studies, and it seems to be still valid today.

One of the difficulties is due to the fact that many sensory inputs are available to direct the behavior of the intact animal. While only one, or a few of these, direct behavior at any given moment, others may take over in short order and in any case play an indirect role by determining the excitatory state of central neurons. A response mechanism with many potential inputs presents a formidable technical problem to the neurophysiologist. For this reason the startle response offers a better chance of analysis since one sensory input overrides all others during its performance.

Another complication lies in the instability of most behavior. This is apparent even in the startle response of the cockroach. If a puff of air is applied a few times in quick succession to a previously undisturbed group of cockroaches the startle response wanes noticeably

and may even disappear. Therefore, it is not surprising that the more labile and rapidly adapting links in the neuron chain for such behavior should fail when the animal is subjected to the gross handling necessary in preparation for electrophysiological experimentation. However, in the case of the startle response in the cockroach it has at least been possible to determine the neural site of this instability and adaptation and to demonstrate some of its properties. The other extreme of this instability is seen in the absence of an equilibrium state in behavior and in the presence of spontaneous activity in many neurons of the insect sensory and central nervous system. The significance of spontaneous activity has been discussed elsewhere (Roeder, 1955), but analysis of its role in behavior has only been begun.

While solutions to these technical problems are being sought, there is another need in this work that has not been met because of the lack of suitably inclined investigators. Physiological studies can never progress far beyond the speculative stage unless they have a firm morphological basis. Thanks to the fine work of Snodgrass and others it is already possible to describe many insect movements in terms of the muscles and articulations concerned. At the same time, there is very little information on nerve distribution and on the finer internal structure of the insect nervous system that is of value in studies of the sort described above. Work of the caliber and viewpoint shown by Power in his series of papers on *Drosophila* (1943, 1946, 1948) would be immensely valuable at this point if carried out on larger insects such as the cockroach and praying mantis. The neurophysiologist is often criticized justly for postulating neurons and nerve pathways which have never been seen. However, when he tries to double as a morphologist he usually finds that he would have been wiser to encourage the interest of a trained specialist. It is my biased opinion that no morphological study could be more interesting or productive at the present time than an examination of the tracts, fiber relations, and synapses in the central nervous systems of the cockroach and mantis. Findings on form could immediately be related to findings on function.

The interaction of prey and predator contains much of interest to other biological specialists. In this paper speed of response has been considered as a primary determinant of the outcome of this interaction, and it has been assumed that speed has been subjected to natural selection. However, it is obvious that many other factors must enter the situation. One such factor, mentioned above, is the accuracy of aim determined during the stalking period. Others, such as the form,

size, or movement of the prey must determine whether the predator shows offensive or defensive behavior and must finally release the strike (Rilling, unpublished thesis). Relative numbers of prey and predator, and the degree to which the odds for survival of either contestant are affected by the outcome, must also play a part. In these areas the neurophysiologist soon finds himself out of his depth. He can only point out that, when compared with contestants in a man-made game, the nervous systems of the insect contestants are relatively simple, and that the outcome has surely been subjected to intense natural selection. Students of evolutionary mechanisms, ethologists, and game theorists might find common and fertile ground in a study of the contest of the mantis and the fly.

SUMMARY

1. The small size of insects and inherently slow impulse conduction in their unmyelinated nerve fibers impose a parsimony or economy of nerve units in their nervous systems. It appears to be necessary that relatively large (and therefore few) nerve fibers mediate neural events in startle responses and predator evasion if insects are to be capable of response times of the same order as those of their vertebrate predators. This means that the neural components of startle mechanisms occupy an amount of central nervous space disproportionate to their complexity.

2. This is illustrated by a description of portions of the neural mechanisms concerned in startle responses in noctuid moths, locusts, and cockroaches.

3. The tarsal flight reflex of flies and the startle responses of noctuid moths, cockroaches, and man all show similar response times which may be causally related.

4. An analysis of the times occupied by the sequence of neural events occurring during the startle response of the cockroach shows that about 10 percent of the total response time is occupied by impulse conduction in axons.

5. The neural processes in the predator while locating, identifying, and stalking its prey must be much more complex than this. This is illustrated by a discussion of prey orientation in the praying mantis. In the mantis the final stage of the attack, the strike, occupies about the same time as the startle response of the potential prey.

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EXPLANATION OF PLATES

PLATE 1

A, cross section of one connective in the abdominal nerve cord of *Periplaneta americana*.

B, distribution of fiber frequency according to diameter. The giant fibers fall into the group between 15 and 30 microns. (From Roeder, 1953.)

PLATE 2

Fig. 1. Schematic frontal section of the left tympanic organ of a noctuid moth. The sensillum (S) contains two sense cells and two scolopes. It is attached to the tympanic membrane (TM) and suspended in the tympanic air sac (TAS) by the ligament (L). The tympanic nerve (TN) carries the pair of acoustic fibers to the *Bugel* (B) and thence out of the tympanic air sac to the thoracic ganglion mass. (From Roeder and Treat, 1957; further details loc. cit.)

Fig. 2. Tympanic nerve response in the moth, *Prodenia cridania*, to a pure tone of 40 kilocycles/sec. After an abrupt onset the tone was continuous throughout each record. The occasional large spike originates in a spontaneously active nonacoustic cell in the ear. A, response to a sound intensity close to threshold for a continuous tone. B, intensity 7 db. above that in A. C, intensity 16 db. above that in A; most sensitive acoustic cell is now firing at maximum frequency. D, intensity 23 db. above that in A; both acoustic cells are discharging and their spikes overlap. Time line, 100 msec. (For further details, see Roeder and Treat, 1957.)

PLATE 3

Fig. 1. Tympanic nerve response in *Prodenia eridania* to a click of 1.0 msec. duration at various intensities. The upper trace in each record shows the electrical pulse which generated the click through a condenser transmitter. A, click is near threshold intensity, and only 1 spike occurs in the more sensitive acoustic unit. B, the same unit fires 3 times at increased click intensity. C, the same unit fires 4 times. D, both acoustic units fire several times with spike overlap at the highest intensity. Time may be judged from the square pulse of 1.0 msec. duration. (From Roeder and Treat, 1957.)

Fig. 2. Bilateral recording from the paired tympanic organs of *Prodenia eridania*. Superimposed responses to 1.0 msec. clicks from condenser transmitter. Clicks delivered at the beginning of trace. Upper trace from right tympanic organ, lower from left organ. A, sound source on right side of moth. B, sound source directly behind moth. C, sound source on left side. Time base, 1,000 cycles/sec.

PLATE 4

Fig. 1. Tympanic nerve response (upper trace) in *Prodenia eridania* to bat cries simultaneously recorded with a condenser microphone (lower trace). The bat (*Eptesicus f. fuscus*) was held 1 to 2 feet from the tympanic organ of the moth. A, an audible "squeak" lasting several milliseconds. B, a shorter cry containing ultrasonic frequencies. (From Roeder and Treat, 1957; details loc. cit.)

Fig. 2. The onset of flight in a calliphorid fly. Upper trace, movements of thorax; lower trace, potential changes in the thoracic muscles. Time marks, 10 msec. intervals. A platform under the feet of the fly was suddenly depressed. Tarsal contact was lost at the lowest point on the upper trace, and the onset of active wing beats are shown by the oscillations at the right in the upper trace. (For further details see Roeder, 1951.)

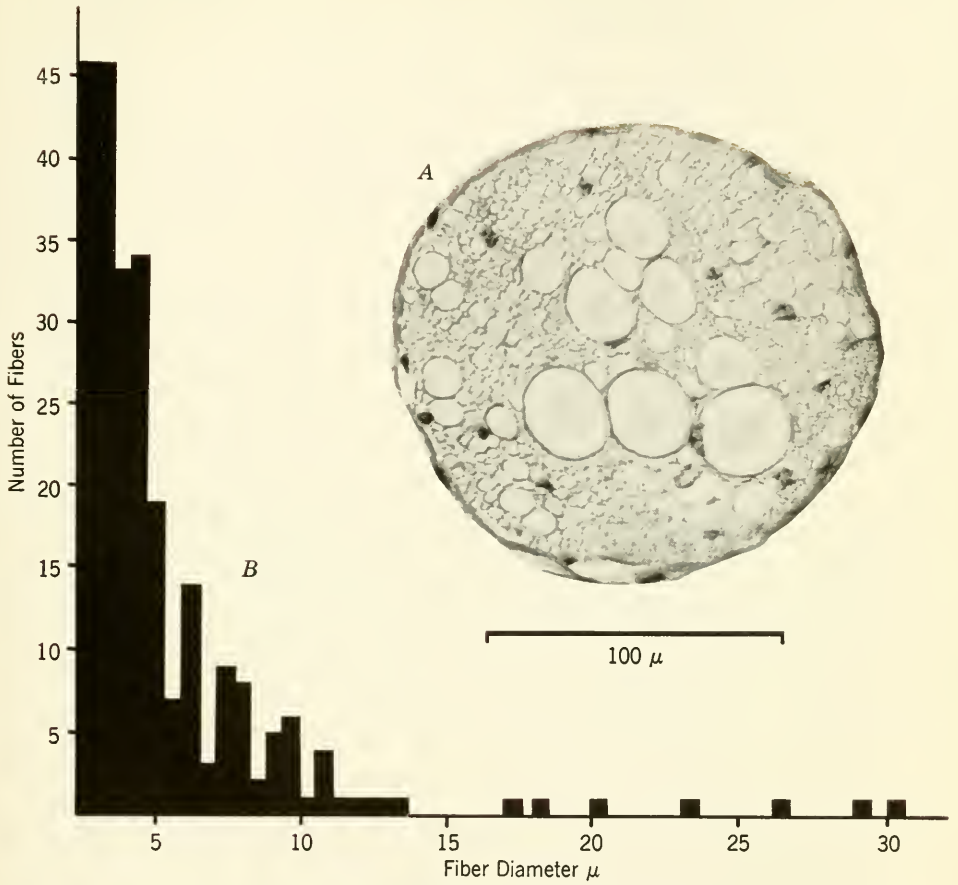
PLATE 5

Conduction in the nervous system of the cockroach *Periplaneta americana*.

A, B, and C. A mechanical stimulus (M.ST.) was applied to the cercus. The movement of the cercus appears as the first upward deflection on the upper trace in A, B, and C. The lower trace in A, B, and C records the arrival of the impulse volley at correspondingly labeled points in the diagram.

D. An electric stimulus (E.ST.) 0.1 msec. in duration was given to nerve 3 close to the metathoracic ganglion. The electric response (lower trace) and contraction (upper trace) of the *extensor tibiae* were recorded at point D.

L.A., last abdominal ganglion; T3, metathoracic ganglion. Time marks for A, B, and C, under C, 1.0 msec. intervals. Time marks for D, 1.0 msec. breaks on upper trace.



(See explanation of plates, p. 305.)

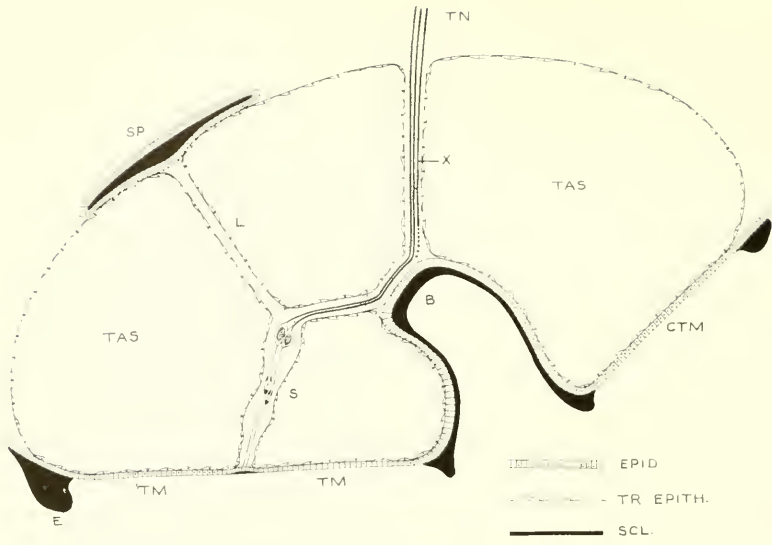


FIG. 1.

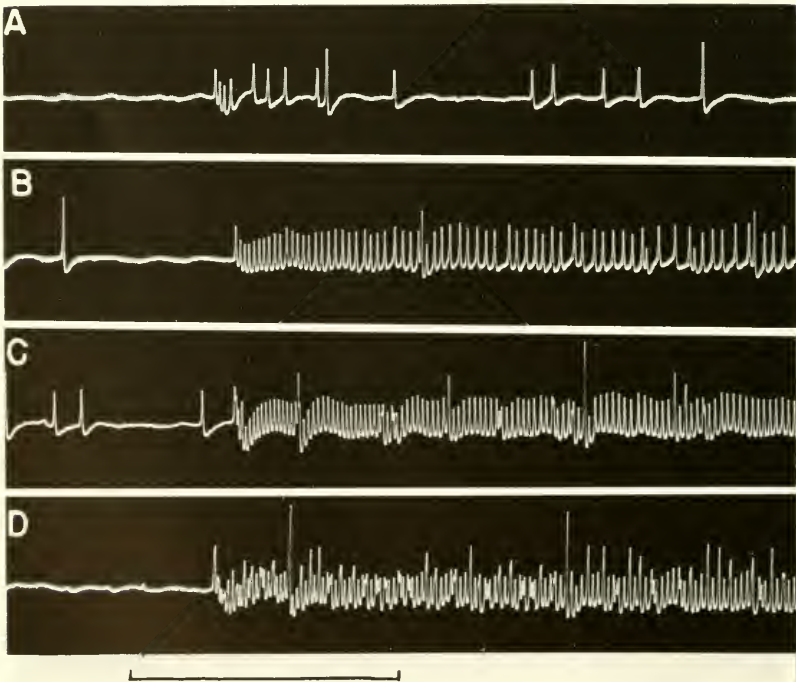


FIG. 2.
(See explanation of plates, p. 305.)

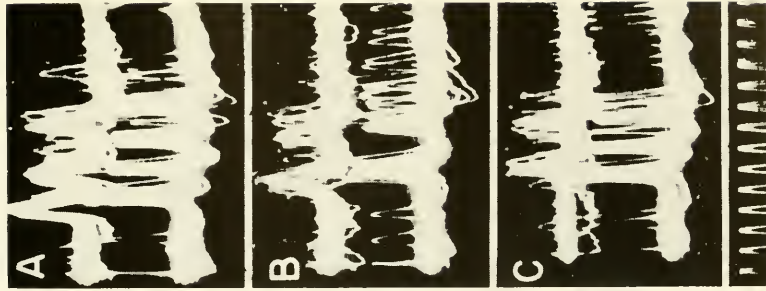


FIG. 2.

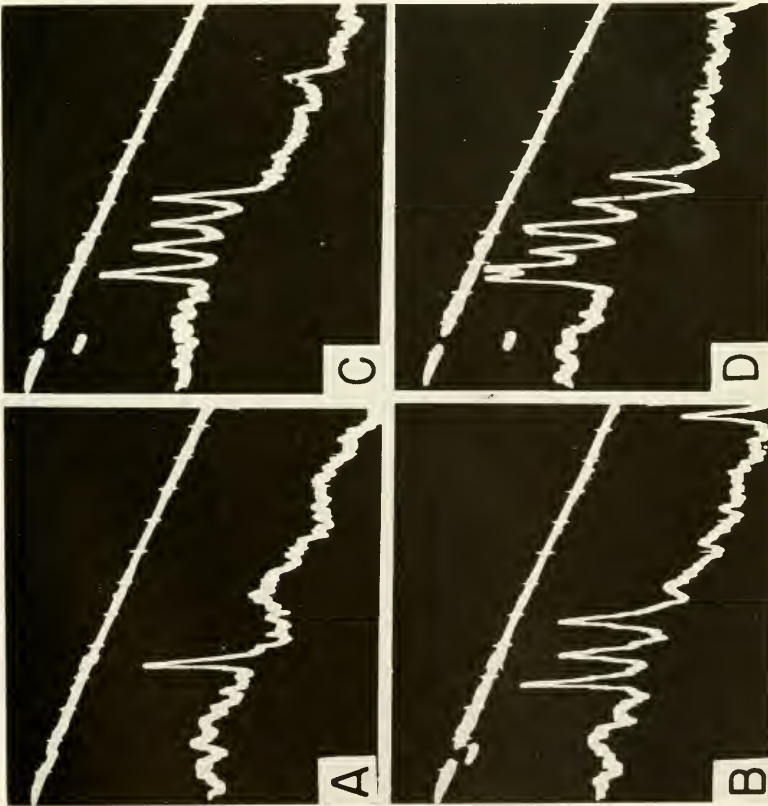


FIG. 1.
(See explanation of plates, p. 306.)

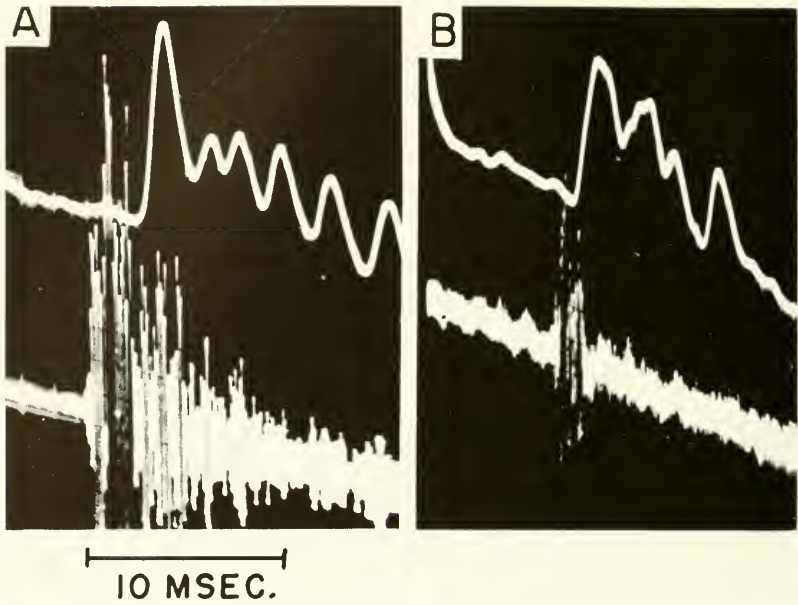


FIG. 1.

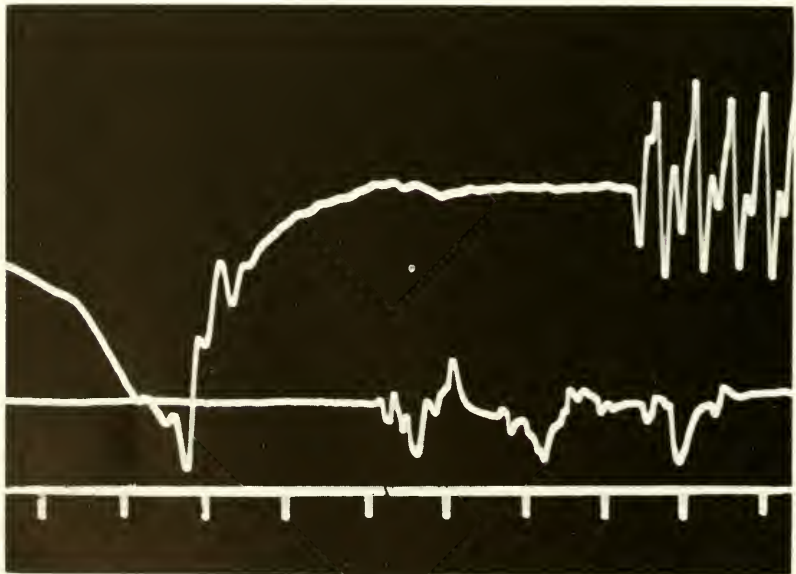
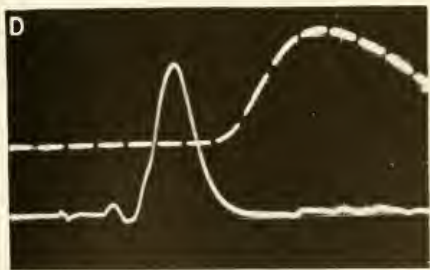
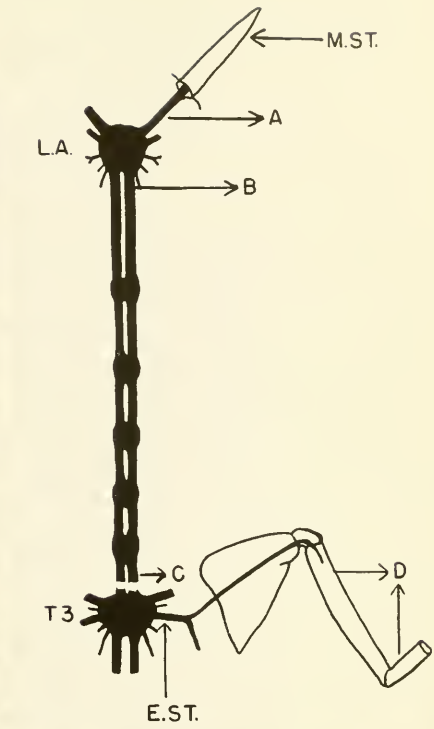
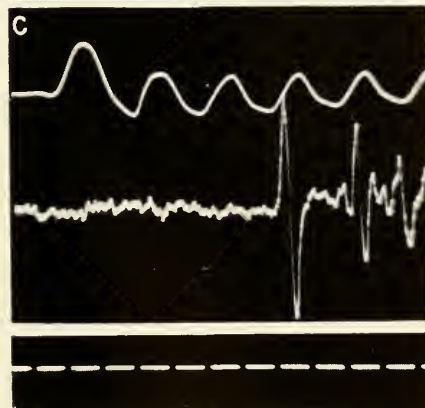
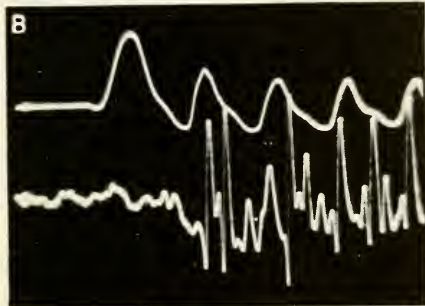
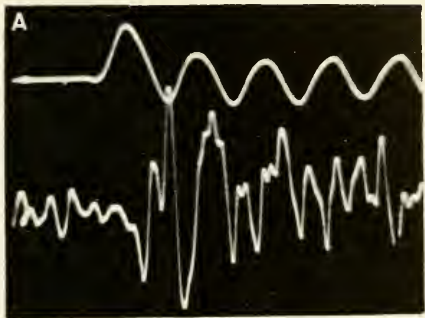


FIG. 2.
(See explanation of plates, p. 306.)



(See explanation of plates, p. 306.)



THE CERVICOTHORACIC NERVOUS SYSTEM OF A GRASSHOPPER¹

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INTRODUCTION

The nervous system of insects has long been a subject for intensive study. The ventral nerve cord and the changes exhibited by it have been described in many forms, at least in its gross aspects, and in more recent years the histology and physiology of the nerves and ganglia have been attacked by many workers. Yet the literature contains relatively few detailed studies of the segmental nerve patterns of insects with respect to the muscle groups innervated. Most textbooks dismiss the subject with only a brief statement to the effect that the muscles of a segment are innervated by lateral nerves from the ganglion of that segment. This paper is, in part, an attempt to supply some information on the arrangement of the nerves with respect to the musculature in the cervix and thorax of a grasshopper, *Dissosteira carolina*. A previous paper by the writer (1954) described the pattern of nerves and muscles in the pregenital abdominal segments of the same insect and of certain other Orthoptera.

Various workers have made detailed studies of muscle-nerve patterns in insects, but attempts to compare such innervation patterns in order to discover segmental features common to several orders have generally been futile, largely because of difficulties in recognizing homologous nerve groups. The concept of an underlying homology of musculature, on the contrary, has been explored to the point of supplying important evidence on the evolution of the insect thorax and appendages. If there was a common ancestral pattern of segmental musculature, an accompanying ground plan of nerves to those muscles seems to be implicit in the concept.

If the innervation pattern as well as the musculature was homologous in each segment of this ancestor, the particular nerve configurations exhibited now in any segment are simply modifications of that original pattern. Since the essential purpose of a nerve is to conduct nerve impulses, there would appear to be less occasion for selective

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pressure resulting in morphological change in the nerve pattern from that source than from changes in the structures served by the nerves.

Many apparent differences in nerve patterns may exist without involving fundamental morphological differences. In one insect, two groups of axones may adopt a common path for a greater distance, or in a second, may separate at a point closer to the ganglion. In the first case, a single definitive nerve results, while in the second, two nerves will be found in a nerve-muscle relationship in which only a single nerve exists in the first insect. A simple example of this may be seen in the segmental nerve patterns of the pregenital abdominal segments of *Dissosteira* (fig. 5 A) and *Diapheromera* (fig. 5 B). In *Dissosteira*, two prominent nerve roots leave the ganglion, but in *Diapheromera*, the same nerve elements are combined and leave the ganglion as a single nerve.

The problem of recognizing homology in nerves thus depends upon the establishment of criteria of homology independent of these definitive disguises. A second objective of this paper is therefore an examination of the nerve patterns of the thorax of *Dissosteira*, to discover, if possible, any such criteria of nerve homologies in the thorax. The writer recognizes, of course, the fact that detailed studies of many more forms are prerequisite to the assured establishing of the scope of any such criteria.

The choice of *Dissosteira* as the insect to be studied arose mainly from the fact that Dr. R. E. Snodgrass has described its skeletal structures and musculature with clarity and precision. His 1929 paper, "The Thoracic Mechanism of a Grasshopper, and its Antecedents," is especially valuable. The groupings, designations, and numbers assigned to the muscles by Snodgrass are employed throughout this paper.

The considerable extent to which morphologically homologous nerves may vary in appearance creates a difficult problem in nomenclature. Some workers have assigned individual names to the nerves of a particular species, as in Korshelt's work on *Dytiscus*, but in most instances such names are of very limited value in comparative studies. Maki (1936) in describing the nervous system of *Chauliodes*, used an elaborate system of roman numerals, lowercase letters, and arabic numerals. The roman numerals designate the "nerve roots" or largest nerves as they leave the ganglion, and successive branchings from the "root" are indicated by appropriate letters and numbers. This is at least a workable system for tentative use in that it is sufficiently flexible to accommodate losses or additions of branches without altering the main designations.

The illustration of nerves and muscles for the purpose of showing patterns and relationships also presents a problem. Realistic figures may show clearly the precise manner in which nerves pass among muscles, but when such figures deal with complex nerve-muscle systems, they often fail to reveal the entire segmental pattern or the relationships believed to provide points of homology. In this paper, an attempt is made to serve these objectives by the use of diagrams which indicate the spatial relationships of the nerves but which substitute numbers for the muscles innervated. The termination of a nerve on the integument is indicated by a short line drawn across the nerve.

I. GENERAL DESCRIPTION

A dorsal view of the cervicothoracic nerve cord of *Dissosteira* is shown in figure 1. The posterior portion of the suboesophageal ganglion usually may be seen projecting slightly from beneath the tentorial bridge. Two fine nerves, the *cervical nerves*, leave the suboesophageal ganglion posterior-laterally and pass dorsally, generally close to the postoccipital ridge.

The paired interganglionic connectives from the suboesophageal ganglion pass beneath the crossed *prosternal muscles of the cervical sclerites* (54) to the prothoracic ganglion. This ganglion lies in a pocket provided by the anterior prosternal plate or basisternum, between the sternal apophyses and immediately anterior to the prothoracic spina. Connectives from the prothoracic to the mesothoracic ganglia pass beneath the *sternospinal muscles* (61), the *second posterior rotators of the prothoracic coxae* (67), and the *third ventral longitudinal muscles* (87), and lie parallel with and just beneath the *fourth ventral longitudinal muscles* (88). The mesothoracic ganglion, like the prothoracic, is located above the basisternum of its segment, between the sternal apophyses and anterior to the mesothoracic spina. The *fourth ventral longitudinal muscles* (88) thus pass just above the mesothoracic ganglion. A pair of fine nerves leaves the dorsal surface of the mesothoracic ganglion and passes to the salivary glands. The definitive metathoracic ganglion lies immediately posterior to the spina and is connected to the mesothoracic ganglion by short connectives which lie on either side of the spina. The *anterior rotators of the mesothoracic coxae* (93) and the *sixth ventral longitudinal muscles* (117), pass immediately above the definitive metathoracic ganglion to their origins on the mesothoracic spina. The ventral nerve cord may thus be seen to occupy a very definitive positional relationship with the ventral skeletal elements of the thorax in *Dis-*

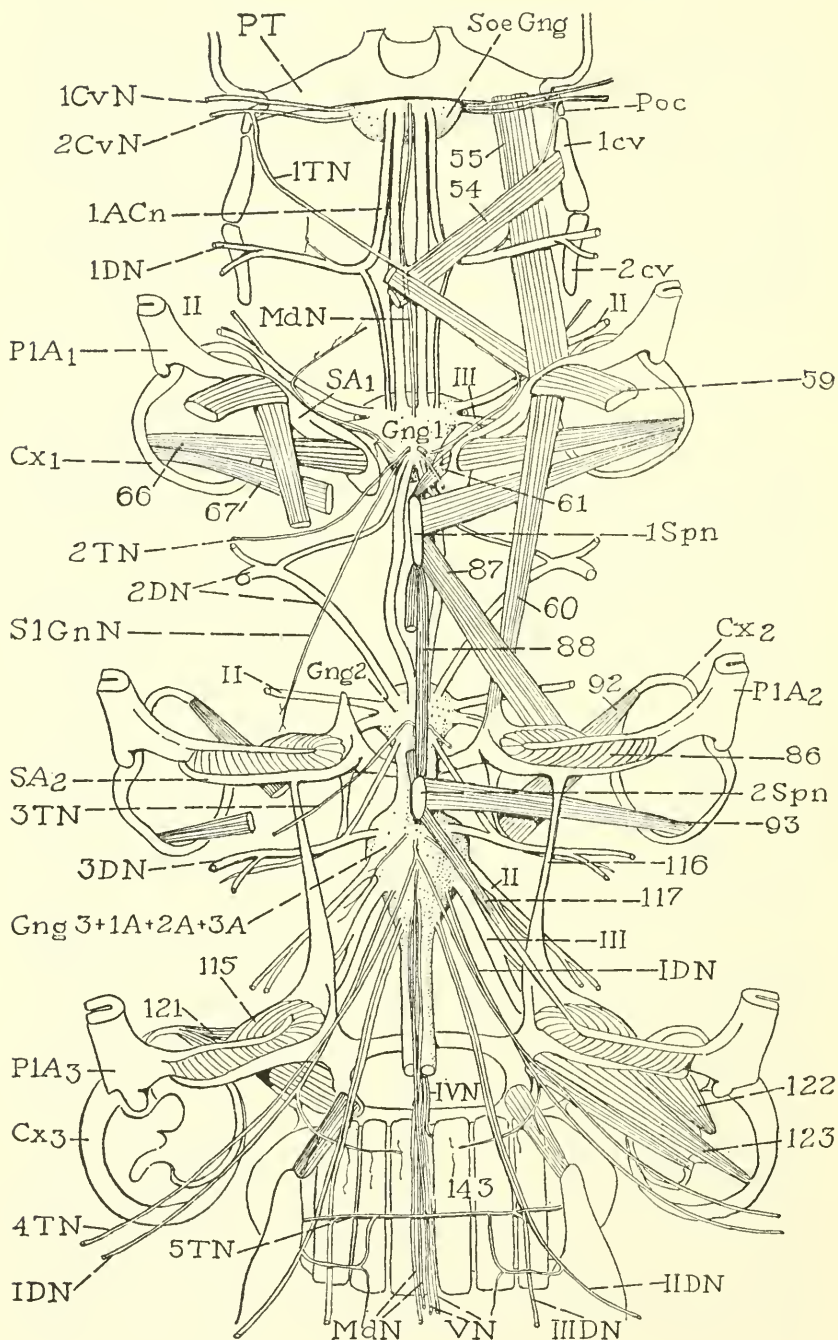


FIG. 1.—General view of the ventral musculature and nerve cord of *Dissosteira* from the head to the first abdominal segment. (Musculature after Snodgrass.)

sosteira. This is especially obvious with respect to the spinae and the muscles attached to these structures, and it seems to be clear that possible future evolution of the ventral nerve cord toward consolidation of the thoracic ganglia will require drastic skeletal and muscle system changes.

II. THE DORSAL NERVE

The mesothoracic nerve system is, in several respects, the most generalized of the three thoracic segments, and is accordingly described first. Three pairs of lateral nerve roots extend from the mesothoracic ganglion. The anterior root, here called the *dorsal nerve* (figs. 1, 2,

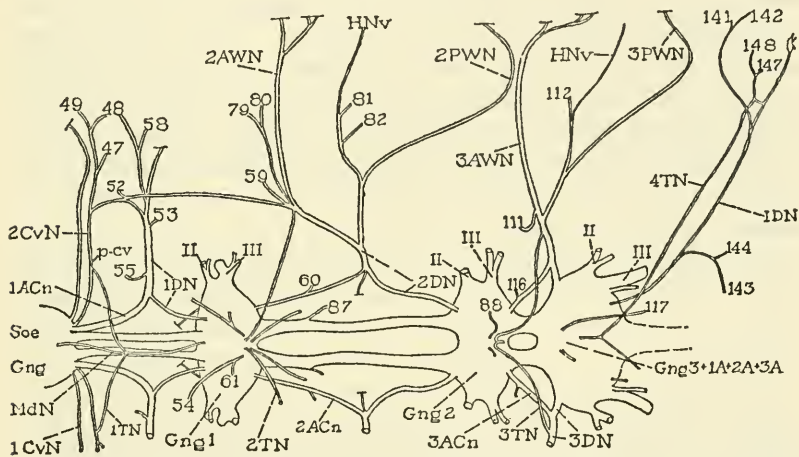


FIG. 2.—Diagram of cervicothoracic median nerves, dorsal nerves, and cervical nerves of the right side, and the innervation of the ventral longitudinal muscles of *Dissosteira*.

2DN), passes under the *second* and *third ventral longitudinal muscles* (60, 87), then passes dorsally along the *tergosternal muscles* (83, 84). An anterior ganglionic connective extends anteriorly from the dorsal nerve to the prothoracic ganglion (figs. 1, 2, *2ACn*), as described by Nesbitt (1941). Near the dorsal nerve junction of this anterior ganglionic connective, a short branch passes to the integument. Just beyond the junction of the dorsal nerve and its connective, a large branch passes anteriorly and provides innervation of the *sternopleural intersegmental muscle* (59) and the *spiracle muscles* (79, 80). The transverse nerve of the median system (fig. 2, *2TN*) joins this anterior branch just proximal of the sternopleural muscle innervation. After providing a second long anterior connection to the prothorax,

this anterior branch of the dorsal nerve becomes the anterior wing nerve (*AWNv*) and enters the tegmen.

The dorsal nerve next provides a large posterior branch which passes mediad of the *tergal promotor of the coxa* (89) and *first tergal remotor of the coxa* (90) to become the posterior wing nerve (*PWNv*). The *dorsal longitudinal muscle* (81) and the *oblique dorsal muscles* (82) receive innervation from the main part of the dorsal nerve, which terminates in a fine branch to the aorta (*HNv*). A similar lateral innervation of the dorsal vessel of the cockroach was described by Alexandrowicz (1926).

The dorsal longitudinal muscles of an insect segment are among the most important morphological "landmarks" in a segment, since their points of attachment may often be used to identify the true intersegmental lines of the primary segment. This use is, in fact, recognition of the antiquity of these muscles as elements of arthropod structure as ancient as the segments themselves. If this concept is true, it follows that the nerves to those muscles must have a corresponding phylogenetic antiquity, and that the elements of these nerves which innervate the dorsal longitudinal muscles in both thorax and abdomen are homologues.

The muscle-nerve patterns of the pregenital abdominal segments of *Dissosteira* (exclusive of the first and second abdominal segments) and of certain other Orthoptera were described by the writer (Schmitt, 1954). A comparison of the nerve entering the dorsal longitudinal muscles of such an abdominal segment with the nerve to the corresponding muscles of the mesothorax reveals a number of points of similarity. The abdominal segment muscle-nerve pattern of *Dissosteira* is shown in diagrammatic form in figure 5 A.

The first point of similarity involves the presence of an anterior branch of the abdominal dorsal nerve from which a branch provides innervation of the spiracular muscles. This pattern was discovered in *Acheta*, *Periplaneta*, and *Diapheromera*, as well as in *Dissosteira*. In the mesothorax of *Dissosteira*, the *spiracular muscles* (79, 80) similarly receive a branch which arises from the nerve that innervates the dorsal longitudinal muscles (fig. 2).

A second point of similarity involves the median or unpaired nervous system in the abdomen and its connections with the branch of the dorsal nerve passing to the spiracular muscles, as shown in figure 5 A, B. The transverse branches of the median system in *Acheta*, *Periplaneta*, and *Diapheromera*, as well as in *Dissosteira*, join this anterior branch of the dorsal nerve. In the mesothorax of *Dissosteira* (fig. 2) no definitive median nerve occurs, but the transverse nerves

of the median system extend from the prothoracic ganglion to the anterior branch of the dorsal nerve. Since these transverse nerves probably contain in their anterior sections some of the same axones which in the abdomen contribute to the anterior part of a median nerve, it appears that precisely the same association of median nervous system and segmental dorsal nerve exists in the mesothorax as in the abdomen.

Maki (1936) shows by his illustrations that a similar arrangement of the dorsal nerve and the transverse nerve exists in both the thoracic and abdominal systems of the alder fly, *Chauliodes formosanus*. The existence of an identical complex in the order Neuroptera shows that this nerve-muscle arrangement is not limited to the Orthoptera, and suggests that it may be of fundamental significance in insect morphology.

In addition to innervating the dorsal muscles of the mesothorax, the dorsal nerve also provides an anterior branch which enters the tegmen anteriorly (fig. 2, *2AWN*) and a posterior branch, entering the same wing posteriorly (fig. 2, *2PWN*). Maki found in *Chauliodes* a nerve, his "fourth root," arising from the anterior part of the mesothoracic ganglion and passing directly, without innervating any muscles, into the wing. Presumably these wing nerves in *Dissosteira* and *Chauliodes* are in fact homologous nerves despite the different routes by which they reach the wing.

III. THE SECOND AND THE THIRD NERVE ROOTS

Unlike the dorsal nerve, the second pair of nerve roots of the mesothorax has no connections with nerves outside that segment. This nerve leaves the ganglion and passes under the ventral longitudinal muscles (figs. 1, 3 A, II). Its first branch innervates the *anterior rotator of the coxa* (92) and part of the *depressor of the trochanter* (103), and a second branch innervates the *abductors of the coxa* (94, 95, 96). The main nerve passes between the *first* and the *second tergo-sternal muscles* (83, 84) and provides innervation for them. The root terminates by innervating the *basalar epipleural muscles* (97, 98) and the *tergal promotor of the coxa* (89).

The third root of nerves is the source of the innervation of all the intrinsic musculature of the leg, as well as of the remaining thoracic muscles exclusive of the ventral longitudinal muscles (figs. 1, 3 B, III). A branch of the third root very close to the ganglion innervates the *sternal remotor of the coxa* (93), a *coxal depressor of the trochanter* (103), the *tergopleural muscle* (85), the *pleurosternal muscle*

A study of the positions of the attachments of the muscles innervated by the second and third root nerves, however, shows an interesting distribution. In general, it may be said that nerves from the second root innervate muscles in the anterior part of the mesothorax, and that nerves from the third root, exclusive of those concerned strictly with intrinsic leg musculature, innervate muscles in the pos-

TABLE I.—*Mesothoracic muscles of Dissosteira innervated by the second root nerves*

Muscle	Sym- bol	Snodgrass number	Origin (or attachment)	Insertion (or attachment)
Tergosternals	C	83	Posterior part of lat- eral prescutal lobe	Anterior part of mesosternum
Do	C	84	Scutum	Mesosternum be- fore coxal cavity
Basalar epipleurals (pronator-extensor of the wing)	E	97	First basalar plate	Lateral part of ster- num before base of leg
Do	E	98	First basalar plate	Anterior part of coxa
Tergal promotor of the coxa	I	89	Scutum	Anterior angle of coxa
Sternal promotor (an- terior rotator of the coxa)	K	92	Sternellum	Anterior angle of coxa
Pleurocoxals (abduc- tors of the coxa) . . .	M	94	Anterior ventral episternum	Anterior outer mar- gin of the coxa
Do	M	95	Do	Do
Do	M	96	Episternum	Lateral margin of the coxa, anterior to pleural articula- tion

terior part of the segment. The depressor of the trochanter is an exception and will be discussed later. Tables I and 2, based on muscle descriptions given by Snodgrass (1929), show the various muscle positions.

A corresponding arrangement of nerves and muscles exists in the metathorax. In the prothorax, the third root nerves innervate the posterior group of muscles as in the pterothorax, but the second root nerves are largely involved in musculature peculiar to the prothorax and will accordingly be considered separately.

TABLE 2.—*Mcsothoracic muscles of Dissosteira innervated by the third root nerves*

Muscle	Sym- bol	Snodgrass number	Origin (or attachment)	Insertion (or attachment)
Pleuroaxillary (flexor of the wing).....	D	85	Pleural ridge	Third axillary sclerite
Pleurosternal.....	G	86	Pleural apophysis	Sternal apophysis
Tergal remotors of the coxa.....	J	90	Scutum	Posterior angle of coxa
Do.....	J	91	Scutum	Posterior angle of coxa
Sternal-remotor (pos- terior rotator of the coxa).....	L	93	Mesothoracic spina	Posterior inner an- gle of coxa
Subalar epipleural (de- pressor-extensor of the forewing).....	E	99	Coxa posterior to pleural articulation	Subalar sclerite
Adductors of the coxa.....	N	100	Posterior of meso- sternal apophysis	Posterior rim of coxa
Do.....	N	101	Mesosternal apophy- sis	Posterior angle of coxa

TABLE 3.—*Mesothoracic muscles of Chauliodes innervated by the second nerve root*

(Data from Maki, 1936)

Maki number	Name of muscle
112.....	1st tergo-sternal
113.....	2d tergo-sternal
114.....	1st tergo-pleural
115.....	2d tergo-pleural
116.....	3d tergo-pleural
117.....	4th tergo-pleural
124.....	Sternal pronator-extensor
127.....	Tergal promotor
133.....	Pleural abductor
134.....	Coxobasalar
135.....	Pleural promotor
138.....	Pleural depressor of trochanter
139.....	Sternal depressor of trochanter

Maki (1936) describes four pairs of lateral nerve roots extending from the mesothoracic ganglion in a neuropteran, *Chauliodes*. A tabulation of the muscles innervated by the second and the third of these roots, as described by Maki, indicates a nerve-muscle arrangement similar to that in *Dissosteira*. Table 3 lists the muscles, as named and numbered by Maki, which he described as innervated by the second root; and table 4 supplies the same data regarding muscles innervated by the third root.

Unfortunately, Maki's figures and text do not indicate the innervation of the *anterior sternal promotor of the coxa* (his 131), but apart from that, it may be seen that in *Chauliodes*, as in *Dissosteira*, two primary innervation patterns exist, one supplying nerves to an

TABLE 4.—*Mesothoracic muscles of Chauliodes innervated by the third nerve root*

(Data from Maki, 1936)

Maki number	Name of muscle
118.....	5th tergopleural
119a.....	Pleuroaxillary
119b.....	Pleuroaxillary
120.....	Epimero-subalar
125.....	Dorsal furco-entopleural
126.....	Ventral furco-entopleural
128.....	1st tergal remotor
129.....	2d tergal remotor
130.....	3d tergal remotor
136.....	Coxa-subalar

anterior segmental group of muscles, and the second supplying nerves to an essentially posterior group of muscles.

IV. THE INNERVATION OF THE MESOTHORACIC LEG

The innervation of the muscles of the mesothoracic leg of *Dissosteira* is provided by the largest branch of the third root. A very fine short branch, just within the trochanter, innervates the *reductor of the femur* (104). The main leg nerve provides two fine branches within the trochanter, both entering the proximal fibers of the *depressor of the tibia* (107). Near its entrance into the femur, the main nerve bifurcates, a branch passing on either side of the depressor of the tibia. Branches of these nerves enter the *anterior levator of the tibia* (105) and the *posterior levator of the tibia* (106). Both of the nerves formed by the bifurcation of the main nerve enter the tibia and provide innervation to the *retractor of the claws* (110). The

lateral of the two branches extends only half of the length of the tibia. The mesal one branches twice to provide three nerves, one of which is closely affixed to the apodeme of the retractor of the claws. A second branch innervates the *levator of the tarsus* (108) and the *depressor of the tarsus* (109), then continues along the ventral wall of the tibia. The third branch proceeds along the dorsal wall of the tibia. Within the tarsus, the ventral nerve ends in profuse branches along the cuticular wall, while the remaining two nerves pass over the *unguitractor plate* and each terminates within a claw.

V. THE CERVIX AND THE PROTHORAX

The cervix or neck of insects is presumably derived in part from the labial segment and in part from the prothoracic. Accordingly, the musculature of the cervical region is believed to have evolved from muscles of both the labial segment and the prothorax. The concept that the muscles of a segment are innervated from the ganglion of that segment suggests that each muscle of the cervix can be assigned to one or the other of these segments simply by determining the segment of innervation of each.

Three pairs of nerves enter the cervix from the suboesophageal ganglion, one pair of which is joined by a pair of nerves from the prothoracic ganglion. An examination of figures 1 and 3 shows that the nerve from the prothorax is obviously a counterpart of the dorsal nerve of the mesothorax and metathorax, and that the nerve joining it from the suboesophageal ganglion is the anterior ganglionic connective of the prothoracic dorsal nerve. The anterior connective is markedly more robust than is the dorsal nerve itself as it leaves the prothoracic ganglion.

The muscles innervated by the prothoracic dorsal nerve presumably include the dorsal longitudinal muscles of the prothorax. However, of the dorsal muscles, only the *tergopleural intersegmental muscle* (58), extending from the protergum to the mesepisternum, is clearly innervated by the prothoracic dorsal nerve alone. The *first* and the *second protergal muscles of the head* (47, 48) are innervated by the second of the nerves entering the cervix from the head, here called the *second cervical nerve*, as well as by the dorsal nerve of the prothorax. These two muscles may therefore represent a fusion of the dorsal longitudinal muscles of the labial segment and the prothoracic. The *longitudinal dorsal muscle of the neck and prothorax* (49) and the *dorsal lateral neck muscle* (56) receive innervation from only the second cervical nerve.

The second cervical nerve and the prothoracic and the mesothoracic dorsal nerves are joined by a definitive nerve which extends from the innervation of the *sternopleural intersegmental muscle* (59) into the cervix, passing mesad of the dorsal nerve of the prothorax, and joined to it by a short connection. A branch from the second cervical nerve marks the anterior end of this definitive nerve.

The fact that the *sternopleural intersegmental muscle* (59) receives its innervation from the anterior branch of the mesothoracic dorsal nerve indicates that it should be considered a mesothoracic muscle rather than prothoracic. In *Chauliodes*, as described by Maki, there exists a similar muscle, the first sternopleural (122), which is innervated in exactly the same manner from the dorsal nerve of the mesothorax, but no anterior extension of the nerve into the cervix exists as in *Dissosteira*.

The remaining muscles innervated by the dorsal nerve of the prothorax include the *protergal muscles of the cervical sclerites* (52, 53), although the innervation of one of these muscles (52) could possibly come from the second cervical nerve. The *first ventral longitudinal muscle* (55) is also innervated by the prothoracic dorsal nerve. The *protractor of the crop* (46), listed by Snodgrass among the prothoracic muscles, is innervated from the ingluvial ganglion.

A very small and insignificant muscle, not figured by Snodgrass and absent in some specimens, extends from the postoccipital ridge to the first cervical sclerite. It is extremely doubtful that this muscle has any utility or function, hence it is here designated simply by position as the postoccipital-cervical plate muscle (fig. 2, *p-cv*). The first cervical nerve passes mesad of this muscle and continues dorsally to enter the cervical integument. The second cervical nerve also passes mesad and provides a small nerve to it.

The second root of nerves in the prothorax innervates six pairs of muscles. Only three pairs of these may be homologized with muscles innervated by the second root in the mesothorax. These include the following: (1) The *tergal promotor* (62); (2) the *abductor of the coxa* (68); (3) two parts of the *depressor of the trochanter* (71).

The writer believes, however, that consideration of the muscles innervated by the third root, together with the fact of the innervation of these muscles by the second root, suffice to show that an organization of these segmental nerves into an anterior root and a posterior root exists in the prothorax as well as in the pterothorax. It appears also that the evolution of the cervix, with a consequent modification and loss of the anterior musculature of the prothorax, accounts for

whatever dissimilarity exists between the second roots in the prothorax and the mesothorax. Five branches of the second root system in the prothorax enter the integument, but corresponding integumentary nerves are absent in the pterothorax.

The musculature peculiar to the prothorax and innervated by the prothoracic second root consists of the following muscles: (1) *Cephalic muscles of the cervical sclerites* (50, 51); (2) *ventral lateral neck muscle* (57).

Perhaps the only point of interest here is the fact that muscles arising on the postoccipital ridge and inserting on the cervical sclerites are unqualifiedly innervated by the prothoracic ganglion.

VI. THE DEPRESSOR OF THE TROCHANTER

The *depressor of the trochanter* (71) is a five-branched muscle inserting on a strong apodeme arising from the base of the trochanter. Two of these muscle branches arise within the coxa and three within the body, as follows: 71a, anterior surface of coxa; 71b, dorsal area of episternum; 71c, pleural arm; 71d, lateral wall of protergum; and 71e, posterior surface of the coxa. The second nerve root provides the innervation of the body branches (71b, 71c, and 71d), and the third nerve root is the source of innervation of the coxal branches (71a and 71e). This dichotomy of innervation occurs also in the pterothorax of *Dissosteira*, and Maki (1936) describes an identical innervation pattern in *Chauliodes*.

It is proposed by Snodgrass (1927) that the division of the depressor of the trochanter in pterygote insects into a coxal branch and a thoracic branch represents two separate muscle sources. It is interesting to note that the innervation pattern of the depressor of the trochanter supports the theory of two primitive muscle sources of the depressor of the trochanter.

VII. THE VENTRAL MUSCLES

The ventral longitudinal muscles are usually assumed to have evolved from primitive ventral muscles comparable to the primitive dorsal longitudinal muscles. In a pregenital abdominal segment of *Dissosteira*, there are three pairs of ventral longitudinal muscles, of which two pairs, the *median internal ventrals* (fig. 5 A, *vim*) and the *lateral internal ventrals* (*vil*) receive innervation from the dorsal nerve as it passes mesad of the muscles. The third pair of muscles, the *lateral external ventrals* (*vel*), are innervated by the second abdominal or ventral nerve (*VN*), passing ventral and lateral.

In the prothorax of *Dissosteira*, the dorsal nerve of that segment passes mesad of the *first ventral longitudinal muscle* (55) and also provides innervation to it, precisely as in the case of the dorsal nerve and the internal ventral muscles in the abdomen. The cervical nerves also pass mesad of the first longitudinal muscle. In the thorax of *Chauliodes*, according to Maki, the prothoracic dorsal nerve passes laterad of the ventral longitudinal muscle, but the two nerves from the suboesophageal ganglion entering the cervix pass mesad as in *Dissosteira*.

In the pterothorax of *Chauliodes*, according to Maki, the dorsal nerves pass laterad of longitudinal ventral muscles and also provide innervation of them, as in the prothorax. In *Dissosteira*, the dorsal nerves of the pterothorax pass laterad of the ventral longitudinal muscles, as in *Chauliodes*, but the innervation of the muscles is at least definitely quite different, both from *Chauliodes* and from the prothoracic and the pregenital abdominal segments of *Dissosteira*.

The *second ventral longitudinal muscle* (60) extends from the prosternal apophysis to the mesosternal apophysis and is listed by Snodgrass as a prothoracic muscle. The innervation of the second muscle is provided by a branch from the anterior connection of the mesothoracic dorsal nerve (fig. 2), suggesting that this muscle should be considered mesothoracic rather than prothoracic.

The *prosternal muscle of the first cervical sclerite* (54) and the *sternospinal muscle* (61) are innervated by a fine nerve which arises from the dorsal surface of the prothoracic ganglion near its posterior end. The *sternospinal muscle* receives a fine branch from this nerve, which then passes along the anterior surface of the pleural apophysis to enter the prosternal muscle. The prothoracic dorsal nerve passes under the prosternal muscle and is joined with its anterior connection to the suboesophageal ganglion just laterad of the point of crossing of the prosternal muscles. The prothoracic dorsal nerve thus may be said to pass dorsally through a triangle of which the first ventral longitudinal muscle forms one side and the crossed prosternal muscles form the other two sides.

The *third ventral longitudinal muscle* (87) extends from the prosternal spina to the mesosternal apophysis. It is innervated by a small nerve which appears to arise from the intersegmental connective between the prothoracic and mesothoracic ganglia. This nerve presumably arises in the mesothoracic ganglion and has become incorporated in the connective simply by being in juxtaposition; attempts to "peel" it away from the connective failed.

The *fourth ventral longitudinal muscles* (88) extend from the first spina to the second spina, passing above the mesothoracic ganglion. A pair of very fine nerves arise from the dorsal surface of the mesothoracic ganglion, each entering the fourth ventral longitudinal muscle of its side.

In its innervation, the *fifth ventral longitudinal muscle* (116) appears to be a homologue of the *second ventral longitudinal muscle* (60). It receives its innervation at its anterior end, from the anterior connection of the metathoracic dorsal nerve, in precisely the manner of the second longitudinal muscle.

The *sixth ventral longitudinal muscle* (117) resembles the *third ventral longitudinal muscle* (87). The metathoracic dorsal nerve leaves the ganglion approximately under the anterior end of the muscle, but morphologically it may be said that the dorsal nerve passes ventrad of the muscle. A pair of fine nerves arises from the dorsal surface of the metathoracic ganglion, entering the sixth ventral muscles near spina.

VIII. THE ANTERIOR GANGLIONIC CONNECTIVES OF THE DORSAL NERVES

The anterior ganglionic connectives of the dorsal nerves have been described in the Orthoptera by Nesbitt (1941). A comparative study of these features of the nervous system indicates that they may have a much wider distribution than merely the Orthoptera but are not recognizable in some cases because of juxtaposition with the connectives of the ventral nerve cord.

The anterior ganglionic connectives (*ACn*) in *Dissosteira* are illustrated in figures 1 and 2. The connective of the mesothoracic dorsal nerve passes under both the *second posterior rotator of the coxa* (67) and the *sternospinal muscle* (61); that of the metathorax passes under the *posterior rotator of the coxa* (93). The route followed by these connectives is thus such that no muscle intervenes between the dorsal nerve connective and the ventral nerve cord, or passes between the connective and the body wall.

In *Dissosteira*, the dorsal nerve connectives leave the ganglia and join the dorsal nerves as structures completely free of the nerve cord. In *Acheta* (fig. 4 A) the prothoracic dorsal nerve connective exhibits a similar condition, but the mesothoracic shows a marked adherence of the connective to the nerve cord. Varying degrees of adherence of both the dorsal nerve connectives and the dorsal nerve may be seen in *Periplaneta* (fig. 4 B) and *Orchelimum* (fig. 4 C). The

metathoracic dorsal nerve and its connective in *Orchelimum* is especially interesting.

Maki describes the thoracic first root or dorsal nerves in *Chauliodes* as arising from the ventral nerve cord, between the ganglia, as shown in figure 4 D. It is, of course, possible that in *Chauliodes* the dorsal nerve is simply adhering to the nerve cord and lacks an anterior connective but the resemblance seen here to the condition in *Orchelimum* suggests that a dorsal nerve connective occurs in the Sialidae. Ham-

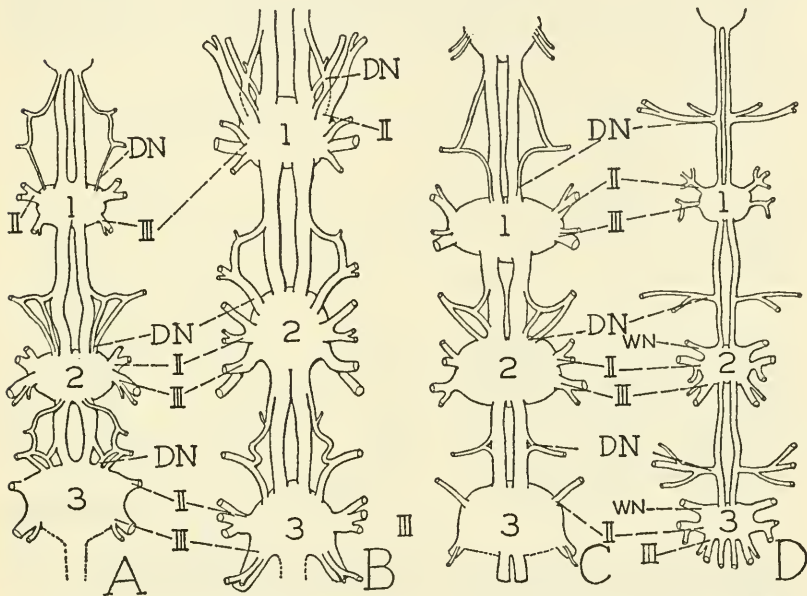


FIG. 4.—Ventral thoracic nerve cords. A, *Acheta* (Gryllidae). B, *Periplaneta* (Blattidae). C, *Orchelimum* (Tettigoniidae). D, *Chauliodes* (Corydalidae, order Neuroptera) (after Maki).

mar (1908) illustrates nerves arising from the ventral nerve cord of the *Corydalid* larva in the same manner. Snodgrass (1925) shows a similar phenomenon in the honey bee.

An anterior connective of the dorsal nerve in the Lepidoptera is illustrated by Weber (1954) in his figure 104, which he credits to an unpublished drawing by H. Nüesch. According to this illustration, the anterior connective of the dorsal nerve contains motor axones extending from the prothoracic ganglion to the dorsal longitudinal muscles of the mesothorax.

IX. THE MEDIAN NERVES AND THE INNERVATION OF THE SPIRACULAR MUSCLES

The median or unpaired nerves of the pregenital abdominal segments following the second in *Dissosteira* are shown in figure 5 A. In these segments, a transverse or lateral nerve leaves the median nerve and extends into the segment on each side, as is usually figured in descriptions of the median nerve system. The definitive end of this lateral nerve joins a larger nerve which branches anteriorly from the dorsal nerve of the posterior segment. The dilator muscle (*dls*) and the occlusor muscles (*osp*) of the spiracle of the posterior segment are innervated by a branch arising from this anterior branch.

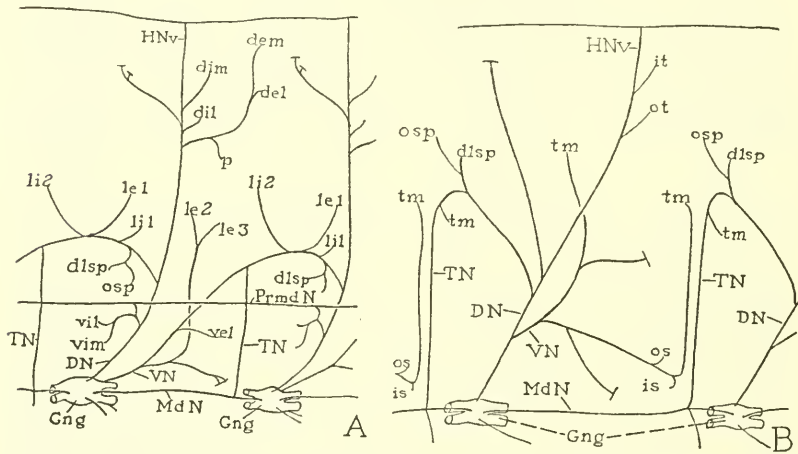


FIG. 5.—Diagrams of the nerve patterns of the right side of typical pregenital abdominal segments, viewed mesally. A, *Dissosteira*. B, *Diapheromera*.

In the walkingstick (fig. 5 B), the cricket, and the cockroach, a similar connection of the transverse nerve with the dorsal nerve and the innervation of the spiracles occurs. Maki (1936) found a similar condition in the abdominal segments of *Chauliodes*. The existence of a definitive connection of the transverse nerve with the dorsal nerve thus occurs in both the Orthoptera and the Neuroptera.

In the thorax of *Dissosteira*, a complete median nerve was found extending from the suboesophageal ganglion to the prothoracic, but not between the remaining thoracic ganglia (fig. 2). A single nerve arises dorsally from the prothoracic ganglion and, passing above the ventral longitudinal muscles, joins the branch of the mesothoracic dorsal nerve which provides innervation of the muscles of the first spiracle and the sternopleural intersegmental muscle (59), and be-

comes the anterior wing nerve. This nerve from the prothoracic ganglion evidently is a combination of the transverse nerve and the median nerve elements of its side of the insect. A similar transverse nerve arises from the mesothoracic ganglion and passes to the metathoracic dorsal nerve. As in the mesothorax, the muscle of the second spiracle receives a fine nerve from the branch of the dorsal nerve, near the junction of the transverse nerve. The dorsal nerves of the first and second abdominal segments also receive paired nerves from the definitive metathoracic ganglion which are clearly the transverse nerves of those abdominal segments (fig. 1).

In the thorax of *Chauliodes*, as described by Maki, the transverse nerves, the dorsal nerves, and the innervation of the spiracular muscles present a pattern identical with that in *Dissosteira*. Moreover, in both insects, there appears to be no essential difference in the innervation patterns of the thoracic spiracles as compared with the abdominal. It is interesting, also, to note that the innervation pattern of the thoracic and the abdominal spiracles makes a continuous series, showing that the thoracic spiracles clearly belong to the mesothorax and the metathorax.

Snodgrass (1935) has presented morphological evidence in support of a theory that the thoracic spiracles of the Pterygota are not homologous with the abdominal spiracles of these insects, but evolved independently of the more ancient abdominal spiracles. According to this concept, the Japygidae, possessing three or four pairs of spiracles in the thorax, retain two pairs of spiracles homologous with the abdominal spiracles, and have also two pairs of spiracles corresponding to the thoracic spiracles of the Pterygota. In view of the fact that in both *Dissosteira* and *Chauliodes*, the innervation patterns of the thoracic and abdominal spiracles are so closely similar, it may be questioned whether the pterygote thoracic spiracles arose completely independent of the abdominal.

The transverse nerve arising from the median nerve between the suboesophageal ganglion and the prothoracic does not join the prothoracic dorsal nerve, but terminates on the second cervical nerve. No explanation of this seeming anomaly has occurred to the writer, unless it means that the second cervical nerve involves separated elements of the prothoracic anterior ganglionic connective which in other segments join the dorsal nerve. If the dorsal cervical longitudinal muscles are derived in part from the primitive dorsal longitudinal muscles of the labial segment, this second cervical nerve should presumably be the dorsal nerve of the labial segment. But the attachment

of the transverse nerve to the second cervical nerve becomes then even more strange, unless we are to suppose that axones from the transverse nerve cross to the prothoracic dorsal nerve (by means of the anterior branch of the prothoracic dorsal nerve) which joins the second cervical nerve. Maki mentions a median nerve issuing from the suboesophageal ganglion in *Chauliodes*, but unfortunately he does not describe its connection sufficiently to permit comparison with *Dissosteira*. Speculation on the significance of this feature of the nervous system is probably futile until further information can be obtained.

In the abdomen of *Dissosteira*, a "ventral nerve" leaves the ganglion posterior to the dorsal nerve, passes beneath the ventral longitudinal muscles, and proceeding laterally and posteriorly, passes laterad of the sternal apodemes to join the anterior branch of the dorsal nerve of the next posterior segment (fig. 5 A, *VN*). The transverse nerve terminates on this ventral nerve-anterior branch loop. In *Diapheromera* (fig. 5 B) the ventral nerve does not join the anterior branch of the dorsal nerve, but the transverse nerve does. Maki found a ventral nerve in *Chauliodes*, but as in *Diapheromera*, it does not join with the dorsal nerve. Although this ventral nerve-anterior branch loop was found in *Acheta* and *Periplaneta*, it evidently is not an essential feature of the abdominal nervous system. The thoracic nervous system of *Dissosteira* does not appear to possess any nerve patterns suggestive of the abdominal ventral nerve.

X. THE DEFINITIVE METATHORACIC GANGLION

It has long been recognized that the ganglion in the metathorax in *Dissosteira* and in many other Orthoptera contains certain abdominal ganglionic centers as well as the true metathoracic ganglion. In *Dissosteira* the abdominal ganglia involved are those of the first three segments. The various nerves leaving the definitive metathoracic ganglion and serving these segments are shown in figure 1, with the exception of the ventral nerves of the left side, which are omitted to reduce the complexity of the figure. The musculature of the abdomen was described by Snodgrass (1935).

As previously noted, the muscles of the pregenital abdominal segments in Orthoptera are served by two main nerves, a dorsal nerve (*DN*) and a ventral nerve (*VN*) (fig. 5). The dorsal nerves of the first abdominal segment leave the ganglion laterally and just posterior to the metathoracic third root (fig. 1). A branch of the dorsal nerve innervates the *median internal ventral muscle* (143) and the *lateral internal ventral muscle* (144). The main dorsal nerve con-

tinues along the large tergal remoters of the coxa and forks just below the tympanum, the anterior fork passing anterior to the first abdominal spiracle to innervate the *lateral oblique intersegmental muscle* (140), the *longitudinal dorsal muscles* (141), and the *lateral oblique dorsal muscles* (142). The posterior fork next provides a fine branch which is joined by the metathoracic transverse nerve and then innervates the spiracle muscles (147, 148). The posterior fork continues as the tympanal nerve to enter Müller's organ.

The ventral nerve leaves the ganglion medially and proceeds ventrally below the main nerve cord. As in other pregenital abdominal segments, it passes beneath the median internal ventral muscles, innervates the *external ventral muscle* (145), the *lateral muscle* (146) which is specialized as the *tensor of the tympanum*, and provides a branch which joins the dorsal nerve of the next posterior segment.

The dorsal nerves of the second and third abdominal segments leave the ganglion side by side and proceed posteriorly together, passing beneath the transverse nerve of the first abdominal segment. Rather strangely, a short connection extends between the third abdominal dorsal nerve and this transverse nerve as the dorsal nerve passes beneath the transverse nerve. A second connection leaves the second abdominal dorsal nerve posterior to this point and provides two branches. The anterior branch connects with the first abdominal transverse nerve; the posterior branch innervates the ventral internal muscles (154, 155) and also marks the anterior end of the paramedian nerve in the female.

A group of lateral muscles, numbered 157 to 164, are described by Snodgrass as differing in many respects from those of the segments following. Three of these muscles, 157, 158, and 160, are innervated by the anterior branch of the dorsal nerve which connects with the ventral nerve of the first segment. In this respect these muscles correspond with the first external lateral muscle, the first internal lateral muscle, and the second internal lateral muscle of the preceding segment. The remaining muscles of the lateral series are innervated by a branch of the ventral nerve, as are the second and third external lateral muscles of the segments following. In most respects, therefore, the innervation of the second abdominal segment presents no unusual aspects.

The median or unpaired systems of the first and second abdominal segments consist of median nerves which terminate in the usual transverse nerves. Only the median nerve of the third segment extends to the following ganglion.

SUMMARY

1. Each thoracic ganglion of *Dissosteira carolina* gives off three pairs of nerve roots. Nerves from the first of these roots innervate the dorsal longitudinal muscles, hence the root and its main nerve is designated as the dorsal nerve. Each dorsal nerve has an anterior connection with the ganglion anterior to it.

2. The nerves from the second root innervate muscles of the anterior part of the segment; nerves from the third root innervate muscles of the posterior part of the segment and of the leg. In these respects *Dissosteira* agrees closely with *Chauliodes* (Neuroptera) as described by Maki (1936).

3. The innervation pattern of the depressor of the trochanter supports the belief that this muscle group originated from two primitive muscles.

4. The cervical musculature is innervated by two fine nerves from the suboesophageal ganglion and by the prothoracic dorsal nerve.

5. The pterothoracic dorsal nerves pass *beneath* the ventral longitudinal muscles, differing in this respect from the prothoracic and the abdominal dorsal nerves of *Dissosteira*, and from all thoracic and abdominal dorsal nerves of *Chauliodes*.

6. The nerves to the thoracic spiracle muscles agree sufficiently with the nerve pattern of the abdominal spiracles to indicate that the thoracic spiracles may be homologous with the abdominal spiracles.

ABBREVIATIONS USED ON THE FIGURES

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| <i>ACn</i> , anterior ganglionic connective. | <i>it</i> , intertergal muscle. |
| <i>AWN</i> , anterior wing nerve. | <i>le</i> , external lateral muscles. |
| <i>1cv</i> , <i>2cv</i> , first and second lateral cervical sclerites. | <i>li</i> , internal lateral muscles. |
| <i>1CvN</i> , first cervical nerve. | <i>MdN</i> , median nerve. |
| <i>2CvN</i> , second cervical nerve. | <i>os</i> , outer sternal muscle. |
| <i>Cx</i> , coxa. | <i>osp</i> , occlusor muscle of the spiracle. |
| <i>del</i> , lateral external dorsal muscles. | <i>ot</i> , outer tergal muscle. |
| <i>dem</i> , median external dorsal muscles. | <i>p</i> , paratergal muscle. |
| <i>dil</i> , lateral internal dorsal muscles. | <i>p-cv</i> , postoccipital-cervical plate muscle. |
| <i>dim</i> , median internal dorsal muscles. | <i>PLA</i> , pleural apodeme. |
| <i>dls_p</i> , dilator muscle of the spiracle. | <i>Poc</i> , postocciput. |
| <i>DN</i> , dorsal nerve. | <i>PrmdN</i> , paramedian nerve. |
| <i>Gng1</i> , prothoracic ganglion. | <i>PT</i> , posterior arm of the tentorium. |
| <i>Gng2</i> , mesothoracic ganglion. | <i>PWN</i> , posterior wing nerve. |
| <i>Gng3 + 1A + 2A + 3A</i> , definitive metathoracic ganglion. | <i>SA</i> , sternal apophysis. |
| <i>HNv</i> , segmental heart nerve. | <i>SIGnN</i> , salivary gland nerve. |
| <i>is</i> , intersternal muscle. | <i>SoeGng</i> , suboesophageal ganglion. |
| | <i>Spn</i> , spina. |

<i>tm</i> , tergosternal muscle.	<i>VN</i> , ventral nerve.
<i>TN</i> , transverse nerve.	<i>WN</i> , wing nerve.
<i>vel</i> , lateral external ventral muscle.	<i>II</i> , second root of nerves.
<i>vil</i> , lateral internal ventral muscle.	<i>III</i> , third root of nerves.
<i>vim</i> , median internal ventral muscle.	

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NOTES ON THE MESOTHORACIC MUSCULATURE OF DIPTERA

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(WITH ONE PLATE)

1. INTRODUCTION

The notes presented below grew out of a study, commenced some years ago, of the morphology of *Anisopus fenestralis* Scopoli (Anisopodidae (=Rhyphidae=Phryneidae), Diptera). This study has not been completed for a number of reasons: First, *Anisopus* did not prove as informative phylogenetically as was hoped; second, *Anisopus* proved somewhat unsatisfactory as an anatomical subject; third, the investigations carried out on *Anisopus* led to some interesting comparative investigations of the musculature of the mesothorax of Diptera in general—the topics of sections 6, 7, and 8 of this paper.

These notes have a common list of references at the end of the paper, and the final concluding comments on the comparative myology and phylogeny of Diptera draw the materials together.

2. HISTORICAL NOTES

The classical works on the musculature of Diptera are the monographic studies of Kunckel (1875-1881) on the drone fly (*Eristalis tenax*) and Lowne (1890-1895) on the blow fly (*Calliphora erythrocephala*). Neither of these works was confined to the musculature, which was treated incidentally to dealing with the entire animal from an anatomical point of view. Furthermore the refinement and artistry of Kunckel's figures and the roughness of Lowne's illustrations both disguise the relative superficiality of their treatment of the musculature, though modern workers should be charitable and keep in mind that these monographs were produced before the Greenough type of binocular dissecting microscope with its erected image was available to the insect anatomist.

Modern studies of flight mechanisms, including only incidentally that of Diptera, taking into consideration both the mechanical and physiological problems involved, were largely initiated by von Lendenfeld (1881-1903) and Voss (1905).

Ritter (1911), a pupil of von Lendenfeld's, published his paper on

"The Flying Apparatus of the Blow-fly" with a subtitle which clearly indicated that his approach was morphological and physiological as well as anatomical.

At about this time Dr. Snodgrass's painstaking and systematic morphological investigations were beginning to influence workers, though their full impact had to await the appearance of his two volumes, "Anatomy and Physiology of the Honey Bee," in 1925, and "Principles of Insect Morphology," in 1935. At about the same time, though commenced a little later and given text-book presentation earlier (1933), the work of the late Dr. Hermann Weber made itself felt in the field of insect morphology.

An important paper resulting from the stimulus supplied by these two masters of the craft of insect morphology was Maki's (1938) monumental work (in English) on the comparative myology of a series of 47 insects. This series included 5 Diptera representing the families Tipulidae, Stratiomyiidae, Syrphidae, Micropezidae (= Calobatiidae), and Muscidae. The very extent of Maki's survey coupled with the difficulties of following his diagrams—he portrays the entire musculature, in a halved insect, as stippled areas, or the origins and insertions of muscles, joined by single lines—has, perhaps served the author ill since one is tempted to feel that a paper covering all the orders of insects could not have details required by a worker confining himself to a single order; the more so when one cannot get specific information quickly from the difficult diagrams.

The study of myology in insects cannot escape a dependence on studies of the exoskeleton. Many workers have, in the past, completely ignored the existence of the soft parts of the insect. Studies of individual insects (e.g., Rees and Ferris, 1939, on a tipulid) are valuable to the comparative myologist. When, however, it comes to selecting insects for myological investigation, the invaluable work is that which has combined study of the exoskeleton with phylogenetic speculation and systematics. Examples of interfertility of work in this field in Diptera are the comparative and phylogenetic studies of the late G. C. Crampton (e.g., Crampton, 1925a, on the thoracic sclerites of nontipuloid nematocerous Diptera) and the relatively few papers in which the late F. W. Edwards (e.g., Edwards, 1926, 1930, Edwards and Keilin, 1928), relying on his own studies and on Crampton's work, allowed himself to indulge in phylogenetic speculations about the Diptera.¹

¹ My own initial selection of *Anisopus* as a subject for anatomical investigation was, in fact, made by reference to the works of Crampton and Edwards.

Dr. Snodgrass himself contributed to our knowledge of the internal anatomy of Diptera in the course of his monograph on the honey bee (Snodgrass, 1925) and elsewhere. But it was not till Partmann (1948) published a paper—with an omnibus title that somewhat obscured the nature of its contents—containing some notes on the anatomy of the mesothoracic, indirect flight muscles of Diptera, that it became apparent that there was something peculiar in the histology and anatomy of these muscles as well as in their possession of the highly specialized physiological properties already recognized (Wigglesworth, 1939; Chadwick *in* Roeder, 1953; Pringle, 1957; and others). Unfortunately Partmann himself did not fully realize what he had discovered, and it remained for the late Prof. O. W. Tiegs to show that the “muscles” comprised in the indirect flight muscles of the mesothorax of Diptera are in the nature of giant fibers and not compact bundles of small fibers (Tiegs, 1955).

Tiegs (*op. cit.*) examined a more extensive series of Diptera than did Maki, and he showed that the anomalies in the musculature² to which Maki had drawn attention were not a peculiarity of the tipulids. This author (1957, 1958) has also added to the information available about these two anomalies.

The general topic of insect flight has recently been reviewed by Pringle (1957).

3. THE THORACIC EXOSKELETON OF ANISOPUS

Figure 1 is a lateral view of the thorax of *Anisopus fenestralis* Scopoli. The figure is on the same scale as figures 2 and 3, which show the extent of the mesothoracic postnotum and its phragma which is partly covered by the metathorax and the first abdominal segment in the lateral external view.

The parts of the exoskeleton of *Anisopus* can be named without much difficulty. The prothorax is complete dorsally and quite distinct from the mesothorax. It has a distinct pleural sulcus; the coxa of the fore leg is large and mobile; well-developed cervical sclerites support the head.

In the mesothorax the dorsum is divided into a gently arched scutum with well-developed posterior callosities and scutellum; articulated to the scutellum is the large postnotum, on either side of which are demarcated the so-called “laterotergites.”

²Maki (1938) had found that his tipulid (1) had a well-developed coxo-subalar muscle, which was not present in the other four Diptera he examined, and (2) lacked the tergal depressor of the trochanter muscle possessed by all the other four Diptera.

In the mesopleural wall there is no difficulty in tracing the pleural sulcus from the true articulation of the coxa to the wing root. In front of the sulcus can be distinguished, using the dipterists' descriptive terminology, an episternal area above and the large sternopleural area below. Whether these two areas are in fact an anepisternum and a katepisternum seems still a matter for debate; Snodgrass (1935)

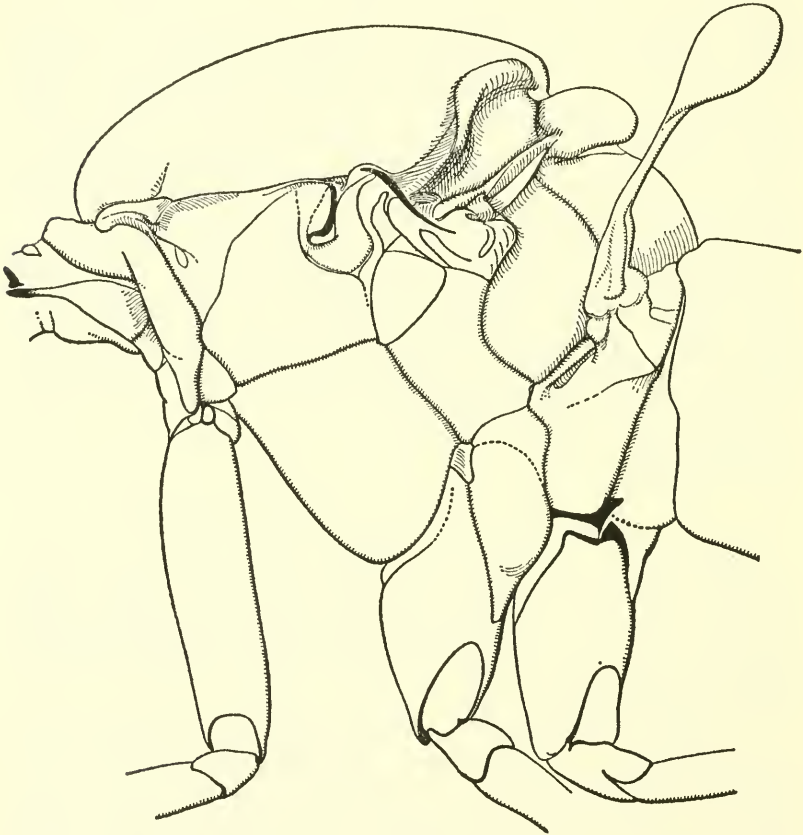


FIG. 1.—*Anisopus fenestralis* Scop., lateral external view of thorax. $\times 42$.

designated the former the episternal area and the latter he called the precoxal area; the sternopleural areas meet in the midline anterior to the invaginated cryptosternum, and the fact that the more anterior dorsoventral indirect flight muscles are inserted on them suggests that they may be composite structures and comprise both episternal and coxal elements which are now indistinguishable. Posterior to the pleural sulcus an anepimeron and a katepimeron can be distinguished.

The basalar sclerite is large, heavily sclerotized, and deeply invaginated. The subalar sclerite is weakly sclerotized and not easily distinguished.

The mesothoracic coxa is large, has a well-developed meron and a very limited capacity for articulation on the thorax. The meron is still part of the coxa and has not become detached, as in higher Diptera, and fused to the thoracic wall to form what the systematic dipterists term the hypopleuron.

The mesothoracic sternum gives rise, at the innermost anterior part of the cleft between the mesocoxae, to a well-developed and heavily pigmented furca.

Anisopus is not a strong flier, and the various sclerites that compose the articulation of wing to thorax are weakly sclerotized and not at all easy to distinguish, a disadvantage when tracing the insertions of the direct wing muscles.

The metathorax bears well-developed halteres; the legs have large coxae and have a free though limited articulation. The lateral elements of the metapleural wall can be distinguished; the dorsum is reduced to a ribbon that passes over the mesothoracic postnotum and is itself in turn covered by the anterodorsal margin of the first abdominal segment.

4. THE MUSCLES OF THE MESOTHORAX OF ANISOPUS

Originally I intended to describe the entire musculature of *Anisopus*. I soon realized, at a date prior to the publication of Tieg's (1955) paper, that the musculature of the mesothorax was not primitive. In particular I could find no trace of the mesothoracic tergal depressor of the trochanter muscle of *Tabanus* (Bonhag, 1949), *Calliphora* (Ritter, 1911), *Drosophila* (Miller in Demerec, 1950), *Psychoda* (Feuerborn, 1927; Dirkes, 1928), *Orthellia*, *Calobata*, *Lathyrphtalmus*, and *Pecticus* (ex. pro *Ptecticus*) (Maki, 1938). A tergal depressor of the trochanter is found in generalized insects such as the locust (Albrecht, 1953), the cockroach (Carbonnell, 1947), and is regarded as one of the basic muscles of the unspecialized pterothoracic segment. It is also present in *Panorpa* (Hasken, 1939), *Boreus* (Füller, 1955), and *Bittacus*, and would therefore be expected in any dipteran with any claims to real primitiveness.

A second purely practical reason for curtailing the work on *Anisopus* was that the weak sclerotization of the exoskeleton coupled with the small size of the creature made it difficult to identify the final insertions of pleural muscle tendons.

The musculature of the mesothorax of *Anisopus* was investigated mainly by dissection under the binocular dissecting microscope. A bold snip with the scissors will split the fly easily down the median dorsoventral line, and one or the other half will usually contain such things as the median furca. Figures 2, 3, and 4 show the steps in a dissection of a half mesothorax; dissections from other approaches were made when investigating the relationships of particular muscles. Most dissections were made of specimens fixed in chlor-picro-acetic fixative³ and stored in 70-percent alcohol. This fixative stains the tissues slightly yellow and it also causes transverse shrinkage of muscles, thus separating them from each other when they are contiguous; it does not cause them to break away from their attachments until dislodged with a dissecting instrument.

Grenacher's alum-carminé stained the small pleural muscles satisfactorily both for dissection and for making transparent whole mounts for examination under the compound microscope. Serial sections were made of a few specimens.

Perusal of recent papers on the musculature of Diptera, e.g., Bonhag (1949) on *Tabanus*, Miller in Demerec (1950) on *Drosophila*, shows that recent workers on the anatomy of Diptera have not found any of the proposed muscle nomenclatures completely acceptable; nor did Maki (1938) at an earlier date, though there are common lines running through the systems of Snodgrass, Maki, and others. The explanation of this state of affairs is obvious; all three thoracic segments in Diptera are so much modified that sooner or later a muscle is encountered that cannot be homologized satisfactorily with those in other thoracic segments—still less with any of the proposed master systems.

I propose to group the muscles of the mesothorax as shown in table 1. Below, in this paper, the muscles are treated consecutively. In figure 4 they are labeled with the numbers they have in the grouping system.

The names used for the muscles in Snodgrass's (1935) general terminology, in that of Ritter (1911) for *Calliphora*, that of Maki (1938) which was a general terminology applied to five different Diptera along with many other insects, Bonhag's (1949) used in his paper on *Tabanus*, and Miller's used in describing the musculature of

³ 60 cc. of a 1-percent solution of picric acid in methylated spirits (i.e., approx. 95-percent alcohol); 10 cc. of chloroform; 5 cc. of acetic acid. Specimens left in fixative for 12 hours or overnight, then washed and stored in 70-percent alcohol.

Drosophila in Demerec's (1950) "Biology of *Drosophila*" are noted. Indications of the synonymy in respect of the terminologies of Snodgrass (1935), Berlese (1909), and of Weber (1928 and 1933) can be found in Nüesch (1953).⁴

TABLE I.—*Mesothoracic muscles of Anisopus*

A.	TERGAL
	1. Dorsal longitudinal.
	2. Oblique dorsal
B.	3. STERNAL
C.	DORSOVENTRAL
	4. Tergosternopleural
	5. Tergomeral
	(6.) (Tergal depressor of trochanter) *
D.	PLEURAL
	(See further, table 2)
	7. Tergopleural
	8. Basalar
	9. Axillary
	10. Coxosubalar
	11. Pleurosternal
E.	LEG
	(See further, table 3)
	(C, 6, above) *
	12. Furcotrochanteral
	13. Coxotrochanteral
	14. Sternocoxal

* Not present in *Anisopus*.

A. TERGAL MUSCLES.

I. DORSAL LONGITUDINAL (INDIRECT FLIGHT) MUSCLES (FIG. 2).

Other names are: Longitudinal median muscles (Snodgrass), dorsal muscles (Ritter), median dorsal muscles (Maki), longitudinal dorsal muscles (Bonhag), dorsal median muscles (Miller in Demerec).

Maki (1938) distinguished between "internal median dorsal" and "external median dorsal" muscles. In Diptera he found the latter present only in *Orthellia* (Muscidae). This distinction is very dubious.

⁴ I have been unable to incorporate much information from Kelsey's (June, 1957) paper on the pterothorax of *Corydalis*. I received the paper in August 1957 but had to proceed on a collecting expedition to New Guinea that same month.

If the "external dorsal" of *Orthellia* did not have its attachment to the scutum demarcated from that of the "internal dorsals" by the transverse suture and the posterior attachment distinguished by being on the postscutellum it could not be distinguished from the "internal dorsals." The transverse suture of the calypterates may not be homologous with that of such Nematocera as possess one (Tipulidae, Trichoceridae, and Tanyderidae); the postscutellum is a feature of the calypterates. Thus the dorsal longitudinal muscles of *Anisopus* cannot be regarded as comprising more than a single series. As noted by Tiegs (1955) these muscles comprise six large "giant" fibers (see elsewhere in this paper).

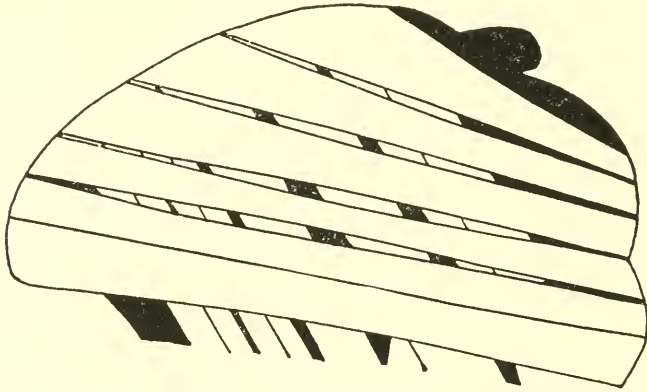


FIG. 2.—*Anisopus fenestralis* Scop., right half of mesothorax at midline to show dorsal longitudinal (indirect flight) muscles. $\times 42$.

The dorsal longitudinal muscles lie on either side of the midline stretching from the scutum to the mesothoracic postnotal phragma. Their action is described as causing depression of the wings, indirectly.

2. OBLIQUE DORSAL (INDIRECT FLIGHT) MUSCLE.

Other names are: Oblique lateral dorsal muscle (Snodgrass), third dorsoventral muscle (Ritter), lateral dorsal muscle (Maki), oblique dorsal muscle (Bonhag), lateral oblique dorsal muscle (Miller *in* Demerec).

When a specimen, split down the midline, has the main dorsal longitudinal muscles removed, this oblique dorsal muscle comes into view along with the dorsoventral indirect flight muscles; it appears to have the same function, acting as an indirect elevator of the wing. It consists of two giant fibers of the same structure as those of the

other indirect flight muscles and is attached dorsally to the posterior region of the scutum and ventrolaterally to the "laterotergite."

Snodgrass (1935) commented on the great development of this oblique dorsal muscle in Diptera. Its hyperdevelopment in Diptera seems to be a characteristic of the group. The muscle is quite small and of a single fascicle in *Telea* (Nüesch, 1953) and *Panorpa* (Hasken, 1939).

There is no trace in *Anisopus* of the third dorsal longitudinal muscle "*dlm₃*" of various authors. Snodgrass (1935) did not distinguish this muscle, which is not surprising. This muscle is small in Megaloptera (Maki, 1936), *Perla* (Wittig, 1955), *Periplaneta* (Carbonell, 1947), *Panorpa* (Hasken, 1939) and other mecopteroids. It is surprising that Maki (1938) claimed to have found this muscle in *Orthellia* (Muscidae); I have not found it in such Muscidae as I have examined.

B. STERNAL MUSCLES.

Other names are: Longitudinal and oblique horizontal ventral muscles (Snodgrass), longitudinal ventral and mesospino-mesofurcal ventral muscles (Maki).

Maki (1938) was uncertain about these muscles in Diptera; he writes of a "common delicate net of ventral transverse muscles" being present in Diptera. Miller in Demerec (1950) says that sternal muscles are present in *Drosophila*; Bonhag (1949) records a "very tenuous fibre" in *Tabanus*. A fine muscle runs from the anterior side of each cup of the mesothoracic furca of *Anisopus* to the endosternal elements of the prothorax; they are extremely easily removed, unnoticed, when the gut is stripped out of a dissection. In position these two muscles are on the midline side of the dorsoventral indirect flight muscles.

In *Anisopus* there appears to be no muscle between the mesofurca and the metafurcal elements.

These sternal muscles obviously have an important part to play in insects where there is some degree of articulation between the different segments of the thorax. It is not surprising that they have become reduced or even lost in Diptera where the prothorax and metathorax have become completely dependent on the very much larger mesothorax.

C. DORSOVENTRAL MUSCLES.

4. TERGOSTERNOPLEURAL (INDIRECT FLIGHT) MUSCLE (FIG. 3).

Other names are: Tergosternal muscle (Snodgrass), 1st dorsoventral muscle (Ritter), anterior tergosternal muscle (Maki), 1st dorsoventral muscle (Bonhag), tergosternal muscles (Miller *in* Demerec).

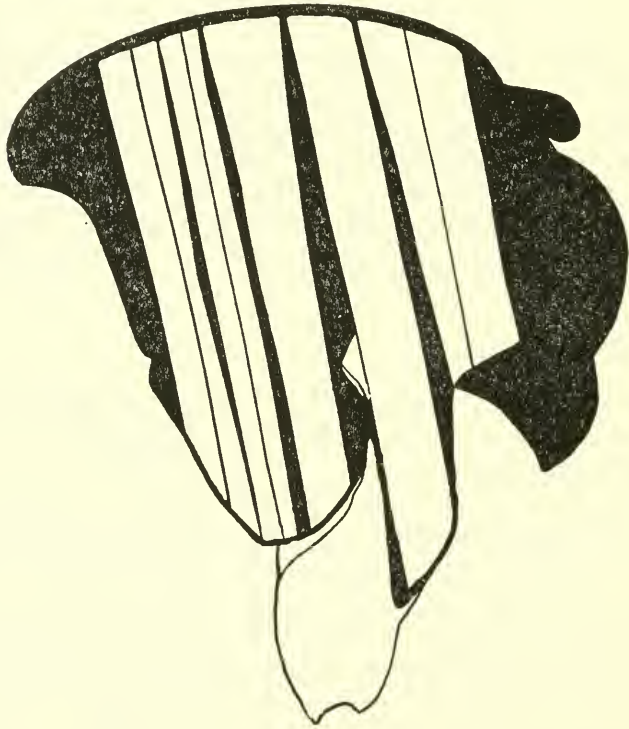


FIG. 3.—*Anisopus fenestralis* Scop., right half of mesothorax with dorsal longitudinal (indirect flight) muscles removed to show dorsoventral (indirect flight) muscles beneath and oblique dorsal muscle beneath. $\times 42$.

This large muscle runs from the tergum to the so-called sternopleuron. It is of the giant-fiber type and, in *Anisopus*, comprises from seven to nine giant fibers. The muscle lies external to the dorsal longitudinal (indirect flight) muscles and anterior to the muscle that connects the pleural wall to the furca (D, 11). The number of fibers may vary on either side of a specimen. It acts as an indirect elevator of the wing.

5. TERGOMERAL (INDIRECT FLIGHT) MUSCLE (FIG. 3).

Other names are: Tergal remotor of leg (Snodgrass), 2d dorso-ventral muscle (Ritter), tergal remotor of coxa (Maki), 2d dorso-ventral muscle (Bonhag), tergal remotor of coxa (Miller *in* Demerec).

This large muscle consists of two or three giant fibers. It lies posterior to the muscles running from the pleural wall to the furca (D, 11) and runs from the scutum to the "hypopleuron" or meron of the mesocoxa. In *Anisopus* the meron, while distinct from the coxa vera, is not completely fused to the pleural wall of the mesothorax and has very little freedom of movement. The muscle acts as an indirect elevator of the wing.

(6). TERGAL DEPRESSOR OF TROCHANTER.

Other names are: Tergal branch of extracoxal depressor of trochanter (Snodgrass), trochanter muscle (Ritter), tergal depressor of trochanter (Maki), (tergal) branch of depressor of trochanter (Bonhag), extracoxal depressor of trochanter (Miller *in* Demerec).

This muscle is not found in *Anisopus*, nor is there any muscle that can be regarded as homologous with it. A general discussion of this muscle as it occurs among Diptera will be found elsewhere in this paper. It is, when present, a muscle of the usual tubular, tetanic type, not of the giant-fiber type like the indirect flight muscles discussed above.

Snodgrass (1935) in the course of his discussion of the generalized musculature of the winged thoracic segment has commented on the condition in the mesothorax of Diptera.

In the generalized winged thoracic segment the following major dorsoventral muscles would be sought for: i, A tergo-sternal muscle (Snodgrass's term); ii, a tergal promotor of the leg (Snodgrass's term) inserting on the trochantin; iii, a tergal remotor of leg (Snodgrass's term) inserting on the posterior rim of the coxa, i.e., the meron; iv, a tergal branch of the extracoxal depressor of the trochanter (Snodgrass's term).

In Diptera, in addition to the oblique dorsal muscle, there appear to be only two large dorsoventral indirect flight muscles. The tergal branch of the extracoxal depressor of the trochanter (C, 6) may be present or absent; it is always readily identified when present, or its absence is obvious.

The great modifications in the general condition of the sternal region of the mesothorax and the disappearance of the trochantin coupled with the lack of any clear subdivision in the tergosterno-pleural muscle had led dipterists to use purely descriptive names to designate the parts thereof.

D. PLEURAL MUSCLES.

The muscles comprised in this group (fig. 4) are all of the usual tubular, tetanic type with the single exception of the coxosubalar muscle (10) which (Smart, 1957) consists of two giant fibers similar to those constituting the main indirect flight muscles dealt with above.

These pleural muscles can be grouped as shown in table 2. In two cases single muscles could be alternatively placed in one or the other of two different groups. These are shown in both possible positions, but in one position the index letter is in parentheses. Below, the muscle is dealt with in the order indicated by the index letter not in

TABLE 2.—*Mesopleural muscles of Anisopus* (Group D in table 1)

- | | |
|-----|--|
| 7. | TERGOPLEURAL |
| | a. Tergobasalar. (See also as 8, c below) |
| | b. Tergopleurosulcal |
| | (c). ? 9, c, i, classifiable here |
| 8. | BASALAR |
| | a. Anterior episternal basalar |
| | b. Inferior episternal basalar |
| | (c). ? 7, a, classifiable here |
| 9. | AXILLARY |
| | a. of 1st sclerite |
| | i. Sternopleural branch |
| | ii. Pleurosulcal branch |
| | b. of 3d sclerite |
| | i. Episternal branch |
| | ii. Lower pleurosulcal branch |
| | iii. Upper pleurosulcal branch |
| | c. of 4th sclerite |
| | i. Pleurosulcal. (See also as 7, c, above) |
| | ii. Epimeral |
| 10. | COXOSUBALAR |
| 11. | PLEUROSTERNAL |
| | a. Superior |
| | b. Inferior |

parentheses; the index letter entry in parentheses shows where it might be placed along with other muscles of related function.

7. TERGOPLURAL MUSCLES (FIG. 4).

Snodgrass (1935) assigned four muscles to this so-named group; they connect the dorsum directly with the pleural wall. There are only three muscles with such a function in the mesothorax of *Anisopus*. The first muscle of Snodgrass's group, his "1B," appears to be missing in *Anisopus*; it is described as running from the "prealar arm of

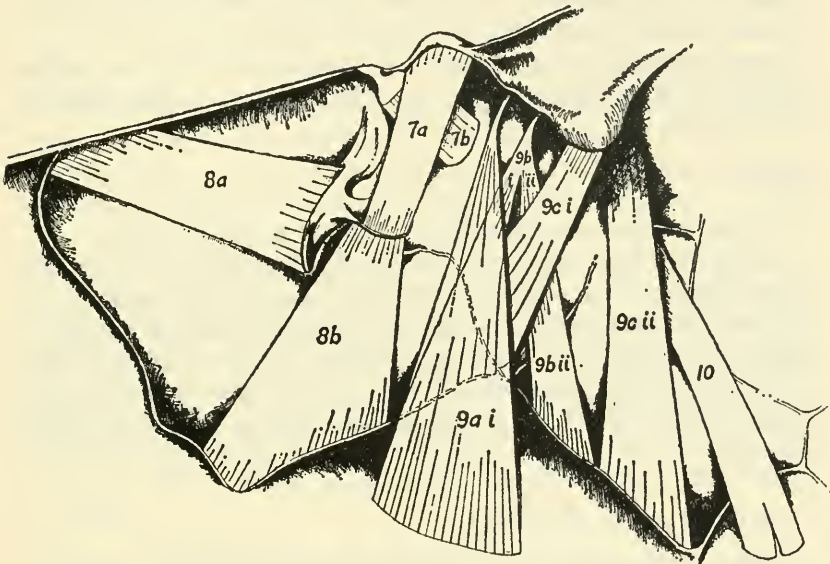


FIG. 4.—*Anisopus fenestralis* Scop., upper part of pleural wall of right half to show muscles related to wing base. Muscles labeled with index numbers and letters used in the text. $\times 84$.

the tergum to the episternum." The specializations of the mesothorax of Diptera have resulted in apparent migration of the origins of the muscles comprised in this group.

a. Tergobasalar muscle.

Other names are: Tergopleural muscle, "2B" (Snodgrass), "musculus gracilis" (Ritter), first pair ordinary tergopleural muscles (Maki), posterior tergal muscle of the basalar (Bonhag), and, possibly, muscle "50" of prealar apophysis (Miller *in* Demerec).

Runs from the anterior notal wing process to the basalar plate.

Specialization of the mesothorax has brought the origin of this muscle into a position posterior to the origin of D, 7, b.

If correctly homologized with Ritter's "musculus gracilis" it is noteworthy that the proportionate size is much larger in *Anisopus* than in *Calliphora*. It could, of course, be grouped with the other muscles inserting on the basalar plate as 8 (c).

b. Tergopleurosulcal muscle.

Other names are: Tergopleural muscle "3B" (Snodgrass), "musculus anonymus" (Ritter), third pair ordinary tergopleural muscles (Maki), tergal muscle of the pleural wing process (Bonhag), and possibly basalar muscle ("52") (Miller *in* Demerec).

Runs from the lateral margin of the scutum to the pleural sulcus on which it inserts just anterior to and below the dorsal wing process of the sulcus.

(c).

As pointed out below, muscle 9, c, i, could be grouped here.

Snodgrass (1935) has a tergopleural muscle, designated 4B, which should run from the posterior notal wing process to the pleural sulcus. No muscle corresponding to this has been described as present in Diptera; I believe that one of the muscles of the 4th axillary sclerite is in fact this tergopleural muscle, 4B of Snodgrass. It is dealt with further below (see 9, c, i: pleurosulcal muscle of the 4th wing sclerite).

8. BASALAR MUSCLES (FIG. 4).

Three muscles attach to the conspicuous basalar plate. One, the tergo-basalar muscle (7, a) has been considered above as a tergopleural muscle. The other two correspond to two of Snodgrass's three epipleural muscles of the basalar plate.

The basalar plate and its system of muscles has, in *Anisopus*, rotated through a full 90 degrees clockwise as compared with Snodgrass's diagrammatic representation of the musculature of the pterothoracic segment (Snodgrass, 1935, fig. 103).

a. Anterior episternal basalar muscle.

Other names are: Epipleural basalar muscle "1E" (Snodgrass), may be "adductor alae secundus" (Ritter), anterior tergal muscle of the basalar (Bonhag), muscle of prealar apophysis ("49") (Miller *in* Demerec).

This muscle runs from the anterior anterodorsal margin of the anepisternum to the anterior face of the basalar plate.

b. Inferior episternal basalar muscle.

Other names are: Sternal basalar muscle "2E" (Snodgrass), "pronator alae" (Ritter), sternobasalar muscle (Maki), pleural muscle of the basalar (Bonhag), basalar muscle ("51") (Miller *in* Demerec).

Maki (1938) and Bonhag (1949) both describe this muscle as double. It is single in *Anisopus* and runs from the line of junction of the sternopleuron with the episternum to the basalar plate.

(c).

As pointed out above, the muscle 7, a, could be grouped with the two preceding muscles inserting on the basalar plate.

There is no muscle running from the basalar plate to the trochanter and acting thereon as an extracoxal depressor thereof.

9. AXILLARY MUSCLES (FIG. 4).

There are three multiple axillary muscles. All have their origins, which in some cases are very broad, on the pleural wall, and all insert on one or other of the sclerites of the wing base. Tension applied to the tendons of insertion must affect the way in which the various articulations work on each other and so, in fact, alter the setting of the wing in the course of its stroke, thus changing the mode of flight of the fly.

a. Axillary muscle of 1st sclerite.

Other names are: Axillary muscle of 1st axillary sclerite (Snodgrass), 1st levator of the wing muscle (Ritter), pleuroaxillary muscle of 1st sclerite (Maki), pleural muscle of 1st axillary sclerite (Bonhag), muscles of 1st sclerite (Miller *in* Demerec).

This muscle is double. The main branch arises on the sternopleuron; a minor branch, not visible in figure 4, originates on the dorsal part of the pleural sulcus. Snodgrass (1935) states that this muscle is found only in Diptera.

b. Axillary muscle of 3d sclerite.

Other names are: Axillary muscle of the 3d axillary sclerite (Snodgrass), 2d levator of the wing muscle (Ritter), pleuroaxillary muscle

of the 3d sclerite (Maki), pleural muscle of the 3d axillary sclerite (Bonhag), muscles of 3d axillary (Miller *in* Demerec).

This muscle has three branches. The largest branch (9, b, i) originates on the episternum, the origin being much occluded by the axillary muscle of the 1st sclerite (9, a, i). A branch of about the same dimensions (9, b, ii) has its origin on the posterior side of the pleural sulcus. The third branch, not shown in figure 4, is a small slip of muscle arising on the dorsal part of the pleural sulcus.

c. *Axillary muscle of 4th sclerite.*

There are two branches of this muscle; they are better considered separately. The weak sclerotization of the region of their insertion in *Anisopus* has made their precise determination difficult and perhaps uncertain.

i. AXILLARY MUSCLE OF 4TH SCLERITE—PLEUROSULCAL BRANCH.

Other names are: Possibly tergopleural muscle "4B" (Snodgrass), 2d supinator (Ritter), 1st tergopleural (pleuroaxillary) muscle of 4th axillary sclerite (Maki), pleural muscle of 4th axillary (Bonhag), and possibly muscles of 4th axillary (sclerite) or axillary cord (Miller *in* Demerec).

This muscle has already been mentioned under 7, c, above. It originates on the pleural sulcus above the point where the sulcus meets the dividing line between the episternum and the sternopleuron.

ii. AXILLARY MUSCLE OF 4TH SCLERITE—EPIMERAL BRANCH.

Other names are: Adductor of the wing ("adductor alae") (Ritter), 2d tergopleural muscle (pleuroaxillary) of the 4th sclerite (Maki), possibly the pleural muscle of the posterior notal wing process (Bonhag), subalar muscle (Miller *in* Demerec).

Maki (1938), dealing with *Orthellia* (Muscidae), and Bonhag (1949), dealing with *Tabanus* (Tabanidae), have indicated a multi-branched muscle in the position of this muscle, though the latter gave its insertion as on the posterior notal wing process. Maki (1938) indicates only a single muscle here in a tipulid. It originates on the epimeron. I consider that this may be the muscle identified by Snodgrass (1935) and Miller *in* Demerec (1950) as a subalar muscle, the former assuming that its origin had migrated from the meron to the epimeron in the "higher Diptera"; this matter is discussed elsewhere in this paper.

10. COXOSUBALAR MUSCLE (FIG. 4).

Other names are: Coxosubalar epipleural muscle "3E" (Snodgrass), coxosubalar muscle (Maki), coxosubalar muscle (Bonhag, but absent in *Tabanus* which he actually described).

This is a specialized muscle as has been pointed out by Smart (1957). It is of the fibrillar type like the large indirect flight muscles of the mesothorax and comprises two giant fibers. Its function has been discussed by Pringle (1957). It originates on the meron of the mesothorax and inserts on the subalar plate. It is not present in *Calliphora* or *Drosophila* and so was not named by Ritter or by Miller *in* Demerec respectively. The coxosubalar muscle is mentioned immediately above and discussed elsewhere in this paper.

11. PLEUROSTERNAL MUSCLES (PL. I, FIG. a).

The cryptosternum of *Anisopus* has a distinctive well-developed furca. The furca has a heavily sclerotized stalk which divides into two arms. The arms are expanded into a large dorsal cup facing upward toward the pleural sulcus and a smaller cup opposite the pleural sulcus at a point just above the articulation of the coxa. The pleurosternal muscles are in fact muscles that link the pleural wall at the sulcus to the cups of the furca. Their function must be largely to hold the pleural wall firmly in position when the insect is flying.

From the underside of the furcal cups there originates the broad-based furcotrochanteral depressors of the trochanter (E, 12).

a. Superior pleurosternal muscle.

Other names are: Pleurosternal muscle (Snodgrass), musculus latus (Ritter), furcoentopleural muscle (Maki), anterior pleurosternal muscle (Bonhag), pleurosternal muscle (Miller *in* Demerec).

This powerful muscle is broadly based on the upper cup of the furca and narrows down to insert along the pleural sulcus. It must have considerable strength, but its shape would indicate that its powerful contraction probably acts only through a very short distance. This suggests that its function is to maintain the position of the pleural wall in relation to the furca rather than to cause any modification in relative positions.

b. Inferior pleurosternal muscle.

Other names are: Pleurosternal muscle (Snodgrass), furcoentopleural muscle (Maki), posterior pleurosternal muscle (Bonhag), pleurosternal muscle (Miller *in* Demerec).

This very short muscle runs between the outer ends of the furcal arms and the lower end of the pleural sulcus. It presumably supplements the superior pleurosternal muscle. Ritter (1911) did not note its presence as distinct from his *musculus latus*.

E. LEG MUSCLES (pl. 1, fig. a).

The muscles operating on the leg above the femur can be grouped as shown in table 3.

The tergal depressor of the trochanter muscle (C, 6; not present in *Anisopus*, see elsewhere in this paper) could be added to the series and thus classified as pertaining to the leg.

TABLE 3.—*Mesothoracic leg muscles of Anisopus* (Group E in table 1)

(C, 6, in table 1)

12. FURCOTROCHANTERAL

13. COXOTROCHANTERAL

- a. 1st anterior levator of trochanter
- b. 2d anterior levator of trochanter
- c. Posterior levator of trochanter
- d. Anterior coxal depressor of trochanter
- e. Posterior coxal depressor of trochanter

14. STERNOCOAXAL

- a. Medial sternocoxal
- b. Posterior sternocoxal

12. FURCOTROCHANTERAL DEPRESSOR OF TROCHANTER MUSCLE (PL. I, FIG. a).

Other names are: Sternal apophysis branch of extracoxal depressor of trochanter (Snodgrass), sternal depressor of trochanter (Maki), mesosternal branch of depressor of trochanter (Bonhag).

A powerful muscle. The cryptosternum is deep and the furca well developed. In *Anisopus* the muscle is large to compensate for the absence of a tergal depressor of the trochanter. In Diptera possessing both, they insert on the same tendon on the trochanter. Maki (1938) mentions a pleural depressor of the trochanter in *Ctenacrosceles* (Tipulidae); he comments on the absence of "pleural levators" of the trochanter in the same fly. I have found the latter but not the former in *Anisopus* and such Tipulidae as I have examined; I cannot help wondering if Maki (1938) made an observational error.

Miller in Demerec (1950) did not find a sternal depressor of the

trochanter muscle in *Drosophila*. A sternal depressor of the trochanter, with its origin on the furca, was reported present by Maki (1938) in all five of the Diptera examined by him; Bonhag (1949) also found a sternal depressor muscle of the trochanter in *Tabanus*. I find that in the specimens of *Drosophila melanogaster* available to me a sternal depressor of the trochanter with origin on the underside of the cups of the furca is present and joins the tergal depressor on the trochanter. It seems possible that Miller in Demerec mistook this muscle for the one which he calls a "sternal remotor" of second coxa (his "65").

13. COXAL TROCHANTERAL LEG MUSCLES (PL. I, FIG. a).

Five muscles in the mesothorax of *Anisopus* can be assigned to this group. Maki (1938) and Ritter (1911) did not consider the muscles of this group.

a. 1st anterior levator of trochanter.

Other names are: Levator of trochanter (Snodgrass), branch of dorsal levator of trochanter (Bonhag), levator of trochanter (Miller in Demerec).

Originates on both the ventral parts of the pleural sulcus and on the coxa below the now almost immobilized articulation of the latter with the former.

It is, however, a single muscle and undoubtedly acts as a levator of the trochanter along with E, 13, b; both insert together on the anterior rim of the trochanter distal to the coxotrochanteral articulation.

Maki (1938) reported a pleural depressor of the trochanter in a tipulid. I suspect that he misidentified this muscle as such.

Miller in Demerec (1950) mentions only one levator in *Drosophila*.

b. 2d anterior levator of trochanter.

Other names are: Levator of trochanter (Snodgrass), branch of dorsal levator of trochanter (Bonhag).

Originates on the anterior rim of the coxa and inserts along with E, 13, a, on the anterior rim of the trochanter distal to the coxotrochanteral articulation and acts as a levator.

c. Posterior levator of trochanter.

Other names are: Levator of the trochanter (Snodgrass), ventral levator of trochanter (Bonhag).

Originates on the posterior rim of the coxa vera immediately opposite the insertion of the posterior sternocoxal muscle (14, b). It inserts distal to the coxotrochanteral articulation on the posterior rim of the trochanter and so acts as a levator.

d. Anterior coxal depressor of trochanter.

Other names are: Depressor of the trochanter (Snodgrass), branch of depressor of trochanter muscle (Bonhag), intracoxal depressor of trochanter muscle (Miller, *in* Demerec).

Originates on the anterior rim of the coxa vera mesad to E, 13, b. It inserts, along with E, 12, and E, 13, e, on the depressor tendon of the trochanter and acts as a depressor of the trochanter.

e. Posterior coxal depressor of trochanter.

Other names are: Depressor of trochanter (Snodgrass), branch of depressor of trochanter muscle (Bonhag), intracoxal depressor of trochanter (Miller *in* Demerec).

Originates on the lower rim of the coxa, mesially, just above the articulating membrane. Inserts, along with E, 13, d, and E, 12, on the main depressor tendon of the trochanter.

14. STERNOCOXAL MUSCLES

There are in *Anisopus* only two muscles in this group.

a. Mesial sternocoxal muscle.

Other names are: Sternal promotor of leg muscle (Snodgrass), ordinary sternal promotor of leg muscle (Maki), sternal promotor of coxa (Bonhag), sternal promotor muscle (Miller *in* Demerec).

A large, thin, flat, fan-shaped muscle originating along the edge of the cryptosternum. It inserts on the anterior wall of the coxa vera and must serve to brace the two coxae together in the midline and give them rigidity in relation to the thorax and so enable the furcosternotrochanter depressor, E, 12, to work with maximum efficiency.

b. Posterior sternocoxal muscle.

Other names are: Sternal remotor of leg muscle (Snodgrass), possibly sternal remotor of the coxa (Bonhag), ordinary sternal remotor of leg (Maki).

Originates on the spinasternum behind the rim of the coxa. Inserts within the posterior rim of the coxa vera immediately opposite the

posterior levator of the trochanter (13, c) and would appear to act to brace the coxa to the thorax.

5. THE INDIRECT FLIGHT MUSCLES OF DIPTERA

It has been recognized for some time (see general texts of insect physiology such as Wigglesworth [1939] and Chadwick *in* Roeder [1953]) that the indirect flight muscles of Diptera are of a special nature and differ thereby from the other thoracic muscles. Snodgrass (1925) commented on them in his book on the honey bee. These muscles have been the subject of much work recently. The following comments and references will serve to give the minimum information immediately needed for the purposes of the present paper, state the position of our knowledge at present, and serve to introduce the reader to the literature if further information is wanted.

The special nature of their physiology has been investigated by Pringle (1949) who comments further on the matter in his book, "Insect Flight" (1957). They are responsible for the extremely rapid vibrations of the thorax that produce the flight movements of the wings.

The indirect flight muscles are usually described as being of a fibrous or fibrillar structure; they give a twitch response to stimuli and are responsible for the extremely rapid thoracic vibrations that give the Diptera their superior powers of flight. Other muscles give a tetanic response to stimuli and are described as tubular.

Partmann (1948) drew attention to the regularity or semiregularity of the division of the great dorsal longitudinal muscles into blocks that, in transverse section, formed a pattern. He suggested that the patterns might have some phylogenetic significance. Tiegs (1955), who unfortunately only discovered Partmann's paper when his own was in press, made the astonishing discovery that these blocks were in fact giant fibers. Tiegs found a maximum of 230 such fibers in the dorsal longitudinal muscles of *Neoratus* (Asilidae) and a minimum of 6 fibers in *Rutilia* (Tachinidae) and several others.

Smart (1957) has shown that this giant-fiber type of muscle is not, however, confined to the so-called indirect flight muscles but that the coxosubalar muscle, when present in Diptera, appears to be of the same nature (see elsewhere in this paper).

6. THE TERGAL DEPRESSOR OF THE TROCHANTER MUSCLE

The following names have been applied to this muscle: Tergal branch of extracoxal depressor of trochanter (Snodgrass, 1935, followed by Miller *in* Demerec, 1950, and others); dorsoventral muscle

4-7 (Weber, 1928, followed by Hasken, 1939, and others, especially workers in Germany); tergal depressor of trochanter (Maki, 1938, followed by Nüesch, 1953; Smart, 1957, 1958; and others); 4th dorsoventral muscle or trochanter muscle (Ritter, 1911); depressor of trochanter muscle (Bonhag, 1949); "long extenseur . . . inséré au trochanter" (Kunckel d'Hercule, 1875-1881); tergal-trochantinal muscle (Kelsey, 1957).

Maki's (1938) term is the most convenient. Below, the muscle will be referred to by the abbreviation TDT muscle. It is not present in the musculature of *Anisopus* described earlier in the present paper.

In Diptera, when present, the TDT muscle is quite distinctive. It originates on the scutum of the mesothorax and inserts on the mesial depressor apodeme of the trochanter of the mesothoracic leg proximal to the axis of the coxotrochanteral articulation. Contraction results in a depression or straightening out of the femur which, if not fused to the trochanter, is attached thereto by a very limited articulation.

The TDT muscle is present in insects possessing a less specialized thorax than the Diptera, and it does seem, in fact, that such a muscle is to be regarded as one of the fundamental muscles of the winged thoracic segment if not of the hexapod limbed thoracic segment regardless of its condition as to wings; Maki (1938) found a TDT muscle present in all the thoracic segments of *Lepisma*.

The condition in the cockroach (*Periplaneta americana*) has been described by Carbonell (1947), and Snodgrass (1952) has concurred with Carbonell's description. According to Carbonell the following muscles act as depressors of the trochanter in the segments of the pterothorax:

A. Inserting on the mesial tendon of the trochanter:

1. Tergal fascicle (135a); origin on tergum.
2. Sternal fascicle (135b); origin on sternal apophysis.
3. Basalar fascicle (135c); origin on basalar sclerite.
4. Coxal fascicle (135d); origin on mesial coxal wall.
5. Coxal fascicle (135e); origin on anterior coxal rim.

B. Inserting otherwise on the trochanter:

1. Posterior coxal depressor (136); origin on posterior rim of coxa; inserts on independent apodeme posterior to mesial tendon.
2. Anterior coxal depressor (137); origin on mesial part of coxa; inserts on independent apodeme anterior to mesial tendon.

(The numbers in parentheses are those used in Carbonell's paper.)

In the mesothorax of the locust or grasshopper (Albrecht, 1953; Snodgrass, 1935, etc.) conditions resemble those found in the cockroach except that there are two muscles with origins on the scutum

and no branch muscle originating on the basalar sclerite. These two muscles insert on the mesial tendon of the trochanter along with two other muscles with coxal origins.

The condition of the muscles in Megaloptera has been reported on by Maki (1936) in *Chauliodes*, by Czihak (1953) in *Sialis*, and by Kelsey (1957) in *Corydalus*. Wittig (1955) has described the condition in Plecoptera in *Perla*.

Maki (1938) states that in *Neopanorpa* (Mecoptera) there is inserted on the mesial depressor apodeme of the trochanter in the pterothoracic segments: (1) a very thick muscle originating on the tergum, (2) a slender fascicle originating on the basalar plate, and (3) a sternal depressor originating on the arm of the furca. Hasken (1939), apparently unaware of Maki's paper, described the same muscles as Maki except that he does not seem to have appreciated that the basalar fascicle inserted on the same apodeme as the tergal and sternal (furcal) muscles; he noted three coxal muscles similarly inserted and two others acting as additional depressors as in the cockroach.

Serial sections of the muscles of the thorax of *Panorpa* show that all thoracic muscles, including the indirect flight muscles, TDT muscle, coxosubalar muscle, and other pleural and leg muscles, are of similar histological structure; they are not separable into two types, fibrillar and tubular, as in Diptera.

Maki (1938) noted the absence of a TDT muscle in the mesothorax of a tipulid and its presence in four other Diptera. He did not record that the literature at the time he wrote indicated that there was a TDT muscle in Psychodidae (Feuerborn, 1927; Dirkes, 1928), as well as in *Calliphora* (Ritter, 1911) and in syrphids (Kunckel d'Hercule, 1875-1881).

Tiegs (1955) noted the condition of presence or absence of this mesothoracic TDT muscle in examples of 11 families of Diptera. Smart (1958) gave an account of a more extended survey of Diptera in respect to this muscle; table 4 is derived from Smart (loc. cit.) with additions.

My examination of an extensive series of Diptera shows that: (1) In Diptera the furcal depressor muscle is, as far as I can ascertain, always present. It is also present in *Panorpa* (Maki, 1938; Hasken, 1939). (2) The basalar depressor muscle is never present in Diptera. It is present in *Panorpa* (Maki, 1938; Hasken, 1939). (3) In Diptera the tergal depressor is either present or completely absent and is a single muscle when present. It is present in *Panorpa* (Maki, 1938; Hasken, 1939). (4) In *Anisopus* and in such other Diptera as have

been considered in the literature in this respect there are not more than two coxal depressor muscles of the trochanter and these insert on the mesial depressor tendon along with the furcal depressor and with the tergal depressor when it is present.

Miller *in* Demerec (1950) pointed out that the TDT muscle in *Drosophila* was a "tubular" muscle similar to the muscles of the pleural wall and not of the fibrillar type like the indirect flight muscles, though it resembled the latter rather than the former in size. This condition holds in other Diptera that possess the TDT muscle.

The "fibrillar" type of indirect flight muscle is characteristic of the Hymenoptera and Diptera (Snodgrass, 1925), and it is therefore not

TABLE 4.—*Tergal depressor of trochanter muscle in Diptera*

(Derived from Smart, 1958)

1. Nematocera *having* TDT muscle: Simuliids, sciarids, psychodids, *Nemopalpus*.
2. Nematocera *lacking* TDT muscle: *Trichocera*, *Anisopus*, *Mycetobia*, tipulids, *Ptychoptera*, *Thaumalea*, culicids, mycetophilids, chironomids, cecidomyiids, blepharocerids, bibionids, scatopsids.
3. Brachycera *having* TDT muscle: Some stratiomyiids, *Tabanus*, *Haematopota*, *Chrysops*, *Pelecorhynchus*, *Scaptia*, rhagionids, therevids, scenopinids, some bombyliids, empids, dolichopodids.
4. Brachycera *lacking* TDT muscle: Some stratiomyiids, *Pangonia*, *Coenomyia*, some bombyliids, asilids, acrocerids.
5. Cyclorrhapha *having* TDT muscle: Lonchopterids, phorids, conopids, all acalypterates examined, *Calliphora*, *Sarcophaga*, *Rutilia*, tachinids, *Oestrus*, *Hypoderma*, *Cuterebra*, *Scatophaga*, muscids, *Stomoxys*.
6. Cyclorrhapha *lacking* TDT muscle: Pipunculids, *Gasterophilus*, *Glossina*, *Hippobosca*.

surprising that no such difference between the TDT muscle and the indirect flight muscles has been reported by those working on the musculature of such insects as the cockroach (Carbonnell, 1947) or the grasshopper or locust (Snodgrass, 1935, etc.; Albrecht, 1953).

There is a TDT muscle in the prothorax and the metathorax of the cockroach (Carbonnell, 1947). Maki (1938) states that he found a TDT muscle in all three segments of *Lepisma*; perhaps the TDT muscle is basic to the general musculature of the hexapod thoracic leg segment regardless of the presence or absence of a wing.

Maki (1938) reported that in the tipulid, *Ctenacroscelis*, there was no mesothoracic TDT muscle (see pl. 1, fig. c), that one was present in the metathorax, and that there was a "pleural depressor of the trochanter" in the prothorax.

In *Anisopus*, which has no TDT muscle in the mesothorax, there

is a perfectly good TDT muscle in the metathorax; the prothorax has an extra coxal depressor of the trochanter that has its origin in a "pleural" situation. In connection with the latter, however, it may be noted that it is very difficult, if not impossible to decide whether the "pleural" part of the prothorax is a downward extension of the tergum or a true pleuron fused-up to the tergum. The prothoracic "pleural" depressor of the trochanter in *Anisopus* may very well be the homologue of the real tergal depressor muscle. There is no such doubt about the metathoracic TDT muscle; its origin is dorsal to the articulation of the halter. Maki (1938) should be referred to for further information on the occurrence of what appear to be TDT muscles in the thoracic segments of various insects.

The physiological reactions of the depressor muscles of the trochanter of the American cockroach (*Periplaneta americana* Linn.) have been commented on by Becht and Dresden (1956); there are indications that the different fascicles have different physiological properties.

Boettiger and Furshpan (1952) have suggested that the function of the TDT muscle in Diptera is to act as a "starter" for the general flying mechanism of the thorax; they were considering *Sarcophaga*, a genus in which the TDT muscle is conspicuous.

When well developed, the morphology of the TDT muscle is very suggestive of its use for jumping, and as such it might conceivably be used at the commencement of flight. This suggestion receives reinforcement when one notices that all the long-legged helicopter-like Nematocera, which certainly do not jump at the commencement of flight, lack the TDT muscle. On the other hand such Nematocera have a remarkable capacity for flying up and down vertically in swarms, though their general mode of flying lacks the rapidity and directional accuracy that is associated with the flight of many Brachycera and Cyclorrhapha.

Not enough is known of the flight habits of other Diptera to be able to comment on the fact that many heavy-bodied, normal-length-legged Diptera also lack the TDT muscle.

Smart (1958) suggested that the mesothoracic TDT muscle in Diptera may be used for distorting the configuration of the thorax and so altering the characteristics of the flight in flies possessing the muscle. It could be used for this purpose when the legs of the fly are hunched up when in flight, as they are in most of the flies that possess the muscle in a well-developed condition. The legs would be hunched up by the levators of the trochanter, and if the point of insertion of

the TDT muscle came beneath the axis of the coxal-trochanter articulation a very strong pull indeed could be exerted by the TDT muscle. The initiation of the return of the trochanter to a position in which the TDT muscle could act as a depressor could be easily initiated by the smaller but doubtless quite effective coxal depressors of the trochanter.

In myogenesis the TDT muscle's origin is associated with the ventral or leg imaginal bud (Zalokar, 1947; Shatoury, 1956). Shatoury has ascribed a very important myogenetic controlling role to the TDT muscle in the development of the indirect flight muscles in *Drosophila*.

The TDT muscle differs in shape in different Diptera. In *Sciara* (pl. 1, fig. *b*) it is long, thin, and nearly columnar. In *Tabanus* it is a well-developed muscle with the origin considerably larger in area than in average cross section and it tapers down continuously to the insertion on the tendon of the trochanter. In *Calliphora* (pl. 1, fig. *e*) the muscle is naturally broader at the base than at its insertion on the tendon of the trochanter, but the diameter is about the same throughout its length. *Musca* (pl. 1, fig. *d*) has a very well developed TDT muscle to which the term fan-shaped can almost be applied.

7. THE COXOSUBALAR MUSCLE IN DIPTERA

A muscle running from the meron of the coxa to the subalar sclerite of the same segment of the pterothorax is generally regarded as one of the basic muscles of the winged segment. In Diptera, Maki (1938) noted the presence of such a muscle in the mesothorax of a tipulid (see pl. 1, fig. *c*) and its absence in the mesothoraces of a stratiomyiid, a syrphid, a micropezid (=calobatid), and a muscid. Tiegs (1955) extended the list, noting its presence in the mesothorax of a tipulid, a culicid, and a chironomid, and its absence in a tabanid, a neme-strinid, a muscid, a syrphid, a bombyliid, a tachinid, a therevid, an asilid, and a drosophilid. Below, it will be referred to by the abbreviation CS muscle.

Bonhag (1949), noting the absence of this muscle in *Tabanus* as contrasted with its presence in a tipulid and Mecoptera, stated his belief that it was "part of the primitive ground plan of the mesothoracic musculature of Diptera."

Details of the CS muscle in *Anisopus* have been given elsewhere in this paper. The CS muscle of Nematocera varies greatly in size. *Ptychoptera* has a very large muscle, and this is associated with an oblique-dorsal muscle that is very much smaller than usual when

compared with the other indirect flight muscles (Smart, 1957). The coxosubalar muscle of *Anisopus* is small (fig. 4, 10).

Smart (loc. cit.) has drawn attention to the fact that the CS muscle in *Anisopus* and *Ptychoptera* is of the fibrillar type similar to the indirect flight muscles, and not of the tubular type like the direct flight muscles of the pleural musculature. In *Panorpa* (Mecoptera) the indirect flight muscles, TDT muscle, CS muscle, and other pleural and leg muscles are all of one histological type and do not appear to be separable into fibrillar and tubular types as in Diptera.

While examining a large number of Diptera for the presence or absence of the TDT muscle (Smart, 1958) I came to the following conclusions about the CS muscle in Diptera: (1) Nematocera which lack the TDT muscle possess a CS muscle. (2) At least some of those few Nematocera which possess a TDT muscle possess a CS muscle. (3) No Brachycera (Brachycera-Orthorrhapha auct.) or Cyclorrhapha (=Brachycera-Cyclorrhapha auct.) possess a CS muscle irrespective of their possession or lack of a TDT muscle.

Snodgrass (1935) says, "In the mesothorax of the higher Diptera the single subalar muscle arises on the lower part of the epimeron dorsal to the meron, but this muscle is probably the usual subalar-coxal muscle transposed from the displaced meron to the pleural wall." From what has been said above it seems that most students of the muscle anatomy of Diptera do not concur with Snodgrass's view on this matter. This reluctance finds some support from the fact that in Nematocera that possess the CS muscle, it is (Smart, 1957) a fibrillar muscle similar to the indirect flight muscles. I suspect that the muscle Snodgrass had in mind when he made the above observation was that now identified in the mesothorax of *Anisopus* as an axillary muscle of the 4th sclerite (D, 9, c, ii).

8. CONCLUDING COMMENTS

The investigations reported upon in these notes were commenced in the belief, frequently mentioned in literature about Diptera (see Introduction), that *Anisopus* was a primitive dipteran and that greater knowledge of its anatomy would prove to be a help in elucidating general phylogenetic problems in Diptera. Soon, however, it became apparent that, in respect to the mesothoracic musculature, *Anisopus* was not primitive.

In the course of the investigation of the musculature of *Anisopus* a considerable number of examples of various families of Diptera were dissected and the relevant literature was examined. Some inter-

esting facts about the coxosubalar muscle (CS muscle below) and the tergal depressor of the trochanter muscle (TDT muscle below) emerged that seemed to have some bearing on phylogeny and relationships of families.⁵ These can be summarized as follows:

1. The bulk of the Nematocera, usually regarded as the more primitive of Diptera, cannot be so regarded. The imagines lack the TDT muscle and have the coxosubalar muscle in a specialized condition; these families are comprised in group 2 of table 4. Many of the flies in this group have helicopter-like flight and are notable for the manner in which they dance up and down in swarms.

2. A small group of Nematocera possess a TDT muscle and, in some cases at least, appear also to have a CS muscle; these are comprised in group 1 of table 4. Crampton et al. (1942) have drawn attention to the fact that in respect of the metanotum the Psychodidae, including *Nemopalpus*, are among the most primitive of Diptera.⁶ It therefore seems possible that the Diptera falling in this group 1 of table 4 are among the most primitive living today. A more detailed comparison of these forms in all instars and their possible relatives would be worthwhile. On the ground they have a scuttling manner of walking reminiscent of *Panorpa* (Mecoptera).

3. All Brachycera and all Cyclorrhapha appear to lack the CS muscle. This is irrespective of the presence or absence of the TDT muscle. These Diptera are in groups 3, 4, 5, and 6 of table 4.

4. In the Brachycera many families and some large, well-defined segregates, usually given status subordinate to that of family (i.e., subfamily, tribe, etc.), possess a TDT muscle. These are the families, etc., comprised in group 3 of table 4.

There are, however, a few families and other subordinate segregates or isolated genera that lack the TDT muscle; these are com-

⁵ In this discussion, as elsewhere in this paper, I am using the following simple classification of Diptera:

NEMATOCERA = Orthorrhapha-Nematocera auct.

BRACHYCERA = Orthorrhapha-Brachycera auct. = Brachycera-Orthorrhapha auct.

CYCLORRHAPHA = Brachycera-Cyclorrhapha auct.

ASCHIZA

SCHIZOPHORA = Muscaria auct.

Acalypterata = Holometopa auct. = Haplostomata auct. + Cordyluridae.

Calypterata = Schizometopa auct. = Thecostomata auct.-Cordyluridae.

The Pupipara cannot be regarded as a natural group, and the families therein must be distributed in the Cyclorrhapha.

⁶ I have been unable to obtain specimens of *Protoplasa* or other Tanyderidae in a condition fit for dissection of the musculature.

prised in group 4 of table 4. Contemplating these, one notes that the groups lacking the TDT muscle are quite isolated from each other and that their apparent immediate relatives are among the groups possessing the TDT muscle and not those lacking it.

5. The bulk of the Cyclorrhapha possess a TDT muscle as is seen by a glance at the families, etc., comprised in group 5 of table 4.

As in the case of Brachycera, the groups lacking the TDT muscle are isolated from each other and, except for the very specialized parasitic pipunculids, they are groups small in number of species and find their apparent immediate relatives among the groups possessing a TDT muscle.

When these facts are contemplated one begins to feel that:

A. The possession or lack of the CS muscle indicates a major systematic division in the Diptera and one of a very ancient evolutionary date, having taken place at a time when all Diptera possessed a TDT muscle. This condition of presence or absence of the CS muscle does, in fact, divide the Diptera into the two main groups, the Nematocera on the one hand and the Brachycera with the Cyclorrhapha on the other.

B. The TDT muscle has been lost by diverse groups at different times in the evolutionary history of the Diptera.

a. In the Nematocera the loss of the TDT muscle is probably of ancient date. It is possible that the group lacking the TDT muscle is monophyletic, i.e., originating from ancestors possessing a CS muscle but which lost the TDT muscle.

b. The nematocerous families in group 1 of table 4 are probably representative of the ancient original Diptera stock possessing both the CS muscle and the TDT muscle.

c. In the Brachycera the loss of the TDT muscle seems to have taken place several times. In some cases this must have happened at a distant evolutionary date since whole families have evolved which lack the muscle. Among these groups lacking the TDT muscle are flies with very specialized habits.

d. Comparatively few Cyclorrhapha lack the TDT muscle. Looking at them from an evolutionary standpoint one feels that probably the loss is of comparatively recent date. The loss also seems to be correlated with specialized habits of one kind or another as in the pipunculids, the tsetse flies (*Glossina*), and *Hippobosca*.

Further comparative studies may confirm the singularity of the Diptera comprised in group 1 of table 4 and convince dipterists that they do in fact represent, albeit in a much modified form, the ances-

tors of all Diptera. If this happens, then it may be necessary to detach them from the Nematocera and set them apart as a new sub-order of Diptera.

The Diptera other than the above group fall clearly into two groups representing two different evolutionary streams. These are, first, the Nematocera in group 2 of table 4 which have retained and specialized the CS muscle but have lost the TDT muscle, and second, the Brachycera together with the Cyclorrhapha, which stream originally lost the CS muscle but retained the TDT muscle.

The existence of these two streams would favor classifications of the Diptera which link the Brachycera and the Cyclorrhapha together rather than those which, relying on the condition of the pupa, etc., attach the designation Orthorrhapha to the Brachycera and thus link them with the Nematocera rather than with the Cyclorrhapha.

The loss of the TDT muscle within the Brachycera and the Cyclorrhapha seems to have been sporadic and to have taken place at various times, and the character cannot be used to effect major subdivisions of either of these groups. Whether subfamilies found to differ from their alleged relatives in this character of the possession or lack of the TDT muscle should be raised to family status or merely confirmed in their subfamilial position is a matter for further consideration when either more fossil evidence is available or comparative studies of both imagines and larvae have been carried out.

9. ACKNOWLEDGMENTS

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I should like to acknowledge the help derived from discussions with numerous workers, more especially with the late Prof. O. W. Tiegs, F. R. S., who was working at Cambridge in 1953-1954, and Dr. T. Weis-Fogh, also in the Cambridge Zoological Laboratories.

10. SUMMARY

The foregoing paper consists of a discussion of some points of the comparative myology of the mesothorax of Diptera. The discussion is based on a preliminary description of the mesothoracic musculature

of *Anisopus fenestralis* Scop. Some tentative phylogenetic conclusions are presented.

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EXPLANATION OF PLATE

PLATE I

Musculature of mesothorax of Diptera.

a, Anisopus. Transverse slice of mesothorax containing the furca, muscles related thereto, and other muscles of leg base; indirect flight muscles removed.

b, Sciara. Dissection of half animal with indirect flight muscles removed and showing long, thin, tergal depressor of trochanter muscle; pleural and leg-base musculature can be seen.

c. Tipulid. Dissection of half animal with indirect flight muscles removed. No tergal depressor of the trochanter muscle. Among the pleural muscles can be seen well-developed coxosubalar muscle.

d, Musca. Dissection of half animal with longitudinal indirect flight muscles and some of dorsoventral indirect flight muscles removed to show well-developed tergal depressor of trochanter muscle.

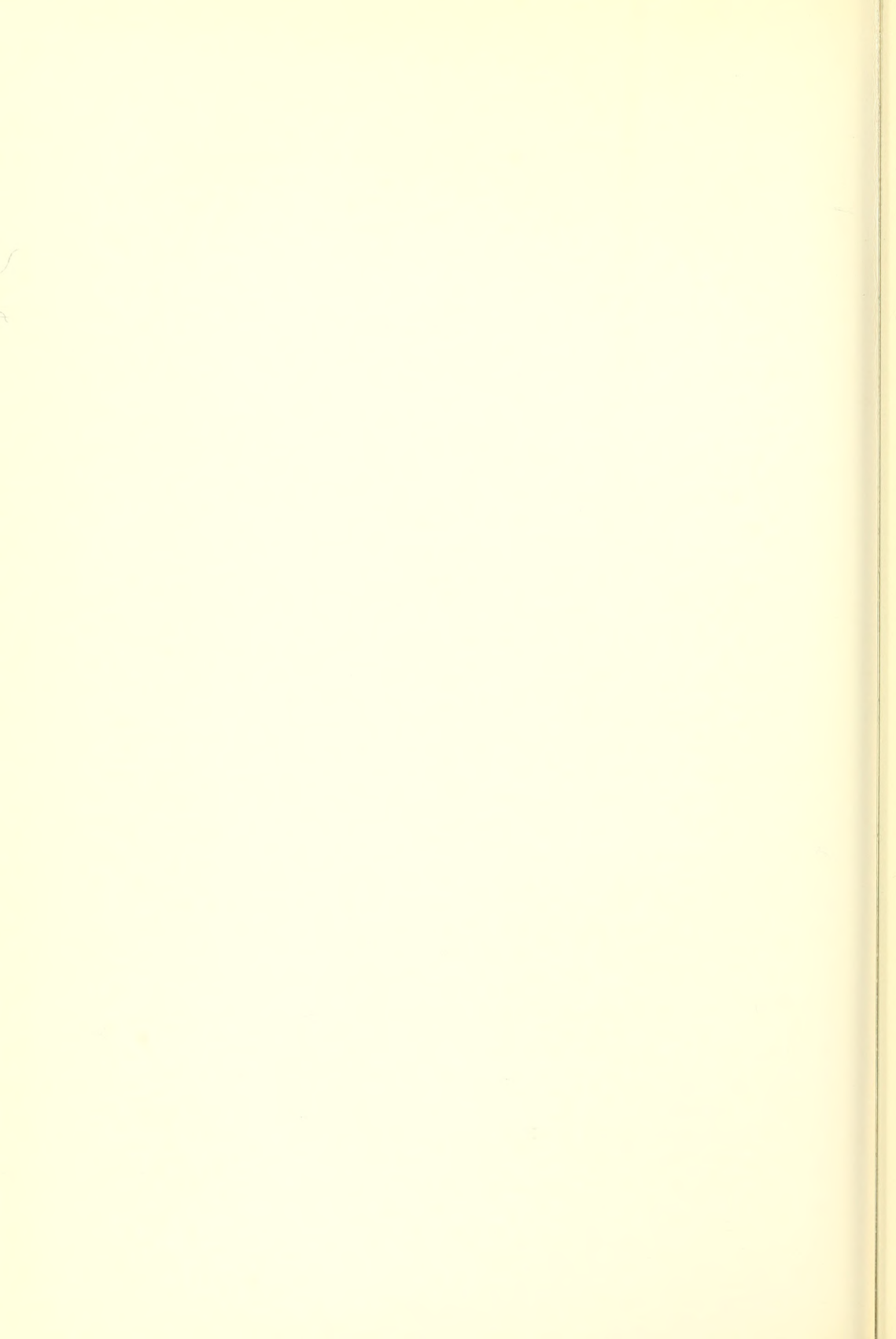
e, Calliphora. Animal cut transversely and indirect flight muscles removed to show position and shape of tergal depressor of trochanter muscles.

f, Glossina. Transverse slice of mesothorax showing furca and muscles related thereto; indirect flight muscles removed.

(Photographs by the author.)



Musculature of mesothorax of Diptera.
(See explanation of plate, p. 364.)



THE METATHORACIC MUSCULATURE OF
CRYMODES DEVASTATOR (BRACE)
(NOCTUIDAE) WITH SPECIAL
REFERENCE TO THE
TYMPANIC ORGAN

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(WITH 16 PLATES)

The most distinctive feature of the noctuid metathorax is the tympanum. Unique among auditory organs in having only two cellular elements specifically concerned with the acoustic response, this structure in its evolution has entailed drastic modifications in the skeletal parts both of its own segment and of the adjacent abdominal region. The integumentary features associated with the tympanum have been described in considerable detail and have entered prominently into current schemes of classification. The histology of the tympanic sensilla has been investigated by Eggers (1919, 1928). Neurophysiological studies (Haskell and Belton, 1956; Roeder and Treat, 1957) have confirmed the impressions of earlier writers that the tympanum is a true acoustic receptor having maximum sensitivity at frequencies somewhat higher than those perceptible to the human ear. It is not yet known, however, whether hearing is the sole or even the chief function of the tympanum, and the work of Roeder and Treat has revealed an active neuronal component of the organ to which no function can as yet be assigned. This element has been found to include a large cell body closely associated with the tympanic sensilla but attached to the surface of the skeletal structure referred to by Eggers and by others as the Bügel. From this neurone is recorded a continuous and apparently spontaneous impulse discharge having no obvious relation to the acoustic response and surviving the destruction of the acoustic sensilla. The discharge frequency may be increased experimentally by stretching the sheath of tracheal epithelium which covers both the Bügel and the tympanic nerve. Could the Bügel cell represent some kind of proprioceptive device, and if so, what might be its relation to the movements of flight or of other behavior? In seeking answers to these questions it appeared neces-

sary to examine in some detail the skeletomuscular anatomy of the noctuid metathorax with special attention to those features pertaining to the tympanum. Though the questions remain unanswered, this paper presents the results of such an examination.

The musculature of the lepidopterous thorax has been described by several writers including Luks (1883), Berlese (1909), Weber (1928), and Maki (1938). More recently Nüesch (1953, 1957) has published brilliant studies of the thorax of *Telea polyphemus*, giving experimental evidence for his detailed conclusions regarding muscle innervation. With the exception of Maki, none of these workers has used a moth possessing a thoracic tympanic organ. Maki included the syntomid *Anata lucerna* Wilem among the insects he examined, but he makes no specific reference to the tympanum and his figure does not permit any precise conclusions as to his findings in relation to that organ. Richards (1933), in his account of the skeletal morphology of the noctuid tympanum, dismisses the muscles with the remark that as regards sclerite homologies, "the modifications brought about by the introduction of the tympanic air sac deprive us of any data ordinarily obtainable from muscle attachments." The sole specific description of tympanic muscles in the literature seems to be a paragraph of Eggers (1919) referring to the three muscles which he found attached to or bordering upon the tympanic air sac in *Catocala*, and which he regarded as forming a firm barrier to further internal expansion of the air sac.¹

¹ "Wie weit die Muskulatur der Umgebung des Organs zu diesem in funktionelle Beziehung tritt, ist aus ihrem Gefüge schwer zu entnehmen. Bei *Catocala* liegen der Tympanalblase drei Hauptmuskeln an. Am auffallendsten erscheint der mittlere von ihnen (*mM*), der durch das Hindurchtreten des Tympanalnerven (*TN*) charakterisiert ist. Der mittlere Muskel zieht quer über die Tympanalblase hinweg, und seine Insertionsstellen sind dorsal der obere Rand des Metascutum (*Mtsc*) und ventral die Muskelleiste (*ML*). In Fig. 9 ist der entsprechende, etwas breitere Muskel (*mM*) von *Diloba* wiedergegeben, wie er, bei günstiger Beleuchtung durch beide Trommelfelle hindurchschimmernd, an der Innenwand der Tympanalblase sich darbietet. Vermutlich handelt es sich um einen Stellmuskel des Hinterflügels. Ein weiterer Muskel, median vom vorigen gelegen, verbindet den oberen Rand des Metascutum mit dem medianen Teil des Rahmens vom Gegentrommelfell und gibt noch ausserdem mehr lateral ein apartes Faserbündel ab, das sich fächerförmig auf der medianen Partie der Tympanalblasenwand ausbreitet. Schliesslich legt sich noch lateral vom mittleren Muskel ein grösserer Hüftmuskel der Tympanalblase an, der gleichfalls am Metascutum beginnend, längs dem Epimeron (*Em*) hinab zur Hüfte zieht. Auf Fig. 9 schimmert ein kleiner Teil dieses Muskels lateral im echten Trommelfell hindurch. Es treten demnach im ganzen drei Muskeln mit dem Organ in unmittelbare Berührung und bilden eine feste Mauer vor der Tympanalblase, die letzterer eine stärkere Ausdehnung nach innen verwehrt."—Eggers, 1919, pp. 304-305.

For the present study the choice of the amphipyridine *Crymodes devastator* (Brace), known in the larval stage as the glassy cutworm,² was dictated chiefly by coincidence. The work was commenced in midwinter when the only material available in sufficient quantity was a collection of formalin-injected moths of this species which had been made the previous summer. Later, moths of a number of other species and families were dissected for comparison, several, especially for the tracheae, in the fresh condition. Most specimens were partly denuded after removal of wings and legs, then hemisected and transferred to 95-percent alcohol for further dissection. For some purposes it was better to have the fixed and hemisected specimen pinned to a block of modeling clay, in air, and moistened from time to time with 50-percent alcohol. Exterior views were drawn from dry, denuded specimens. Skeletal parts were studied and drawn from KOH-cleared specimens prepared in the manner described by Richards (1933). Several tympana were excised, cleared, and mounted on slides for special study of the Bügel and associated parts.

As regards the skeletal homologies of the tympanic region, the views of Richards are accepted provisionally. Richards's ascription of postnotal origin to pockets II and III gains support from the clear serial homology between muscles IIId₂ and IIIId₂, the former arising from a lateral tendon plate or phragma-like process of the mesopostnotum, the latter from what appears to be an anterior extension chiefly of the inner wall of pocket III, referred to by Eggers as the Muskelleiste, and here designated the anterior tendon plate (pls. 2, 12, ATP). Some confusion may arise from Richards's remark concerning the Bügel that although it is prominent in *Catocala*, "none of the other genera examined possess such a structure." Taking the term Bügel to mean (in the noctuids) any apodemal ingrowth from the tympanic frame which serves as a central anchor for the tympanic sensillum or nerve on its course through the tympanic air sac, it may be said that no species thus far examined by the present writer lacks the Bügel completely, and that in most species the structure is fairly prominent, as it is in *Crymodes*. Histological and physiological details regarding the Bügel cell will appear in another publication.

The muscle figures were drawn directly from dissections, but are

² This species was described by Brace in 1819 as *Phalaena devastator*. It is figured in Holland ("The Moth Book") as *Hadena devastatrix*. Forbes (1954) assigns it to the genus *Septis*, which he includes in the tribe Septidini of the subfamily Acronyctinae. The nomenclature used here is that of McDunnough (1938), which is probably familiar to most entomologists.

semischematic in certain respects such as (1) the stylized treatment of muscle fibers and tracheae, (2) the predominance of black-on-white stippling for the shading of the external surfaces, and (3) of white-on-black stippling for internal skeletal surfaces. The drawings were essentially finished before Nüesch's publications had come to hand; otherwise some of his conventions might have been adopted in preference to those actually employed.

The terminology is mainly that of Nüesch and hence is derived from Weber. Nüesch (1953) has identified the muscles of *Telea* with their presumed homologues in the insects studied by Snodgrass and other writers. It seems possible to homologize virtually all the metathoracic muscles of *Crymodes* with those figured by Nüesch, and independent comparison with the figures and descriptions given by other authors yields results which are in full agreement with Nüesch's conclusions.

In the description that follows, the muscles are arranged according to the Weber-Nüesch scheme of classification which is based wholly upon anatomical position and avoids commitments as to action. In many instances the actions may be inferred from the attachments or may be supposed to be as indicated in Snodgrass's classification (1935) which is followed in table 1. Direct electrical stimulation of some of the main muscle groups was attempted in a few living noctuids (not in *Crymodes*) but revealed nothing novel or of special significance. Possible actions of the muscles associated with the tympanum will be considered in the discussion.

MUSCLES OF THE METATHORAX

Dorsolongitudinal muscles

- dl*_{1a} Plates 5, 12, 16. The separate, fan-shaped fiber bundle of the most median of the three muscles described by Eggers (see footnote 1). A broad bundle arising on the surface of the prescutum just lateral to the origin of *dl*_{1b} and inserting more or less fanwise on the dorsomedial sclerotization of the tympanic air sac. Note that the prescutum is flexibly hinged by its soft dorsal portion to the anterior margin of the scutum and thus does not afford a rigid attachment for the fibers of this muscle.
- dl*_{1b} Plates 5, 10, 12, 16. The most median of Eggers's three muscles, exclusive of his separate fan-shaped bundle (see *dl*_{1a}). A narrow fan, diverging from the dorsomedial angle

of the prescutum to the median ridge or keel of the metapostnotum beneath the countertympanic septum.

- dl₂ Plates 5, 8, 9, 12, 13, 14, 16. Eggers's middle muscle (*mM*). A thick band from the central portion of the scutum to the posterolateral surface of the anterior tendon plate (Eggers's *Muskelleiste*) of the tympanic frame (Nüesch's "lateral tendon plate of the postnotum"). Its fibers lie medial to the tympanic twig of nerve *IIIN1b*, from which nerve it also receives a twig.
- dl₃ Plates 10, 12, 16. A thin, pulsatile membrane stretched more or less obliquely across the interior of the metascutellum in each of its lateral arms, bordering ventrally upon the haemolymph channel communicating with the axillary cord of the hind wing. Probably not homologous with *IIdl₃*, but corresponds to Brocher's (1919) membrane *p*.

Ventrolongitudinal muscles

- vl₁ Plate 10. A long, subcylindrical band from the caudal surface of the anterior furcal arm to the fused sterna of abdominal segments 1 and 2.
- vl₂ Plates 6, 9, 10, 12. A short bundle from the dorsal surface of the posterior tendon plate of the tympanic frame (?post-coxal bridge) to the ventral surface of the first (+second) abdominal furca near its tip. May be homologous with the Bügelmuskel of von Kennel and Eggers (1933, p. 26) in the geometrids.

Dorsoventral muscles

- dv₁ Plates 10, 12. A narrow band from the anterolateral angle of the scutum, medial to the anterior wing process, to the basisternum just lateral to the ventral median plate. Portions of both left and right muscles are shown in the figures and are labeled *L* and *R* respectively.
- dv₂ Plates 8, 12. A long band from the scutum, just posterior to the origin of *dv₁*, to the anteromedial angle of the coxa, parallel to *dv₁*.
- dv₃ Plates 7, 8, 12, 13, 16. Two thick bundles converging from the scutum anterior to *dv₄₍₅₎* to the median (depressor) tendon of the trochanter. According to Nüesch, this muscle in *Telea* is also divided at its dorsal origin.
- dv₄₍₅₎ Plates 6, 7, 8, 9, 12, 13, 14. A stout bundle, not obviously

subdivided (into dv_4 and dv_5 as in *Telea*), from the scutum posterior to dv_3 to the ventrolateral portion of the meron. Flanks dl_2 anterior to the tympanic air sac. This is the most lateral of the three muscles described by Eggers.

Pleurodorsal muscles

- pd_1 This muscle, as well as pd_4 and pd_5 , appears to be absent in the metathorax, as in *Telea*.
- pd_{2a} Plates 7, 15. A stout, rectangular band from the pleural wing process to the tendon of pd_{2c} , inserting on this tendon, approximately at right angles to it, and on the 3d axillary sclerite.
- pd_{2b} Plates 6, 7, 12, 14, 15. A thick band from the dorsolateral portion of the episternum just ventral to the basalare, to the 3d axillary sclerite.
- pd_{2c} Plates 6, 7, 14, 15. A thin fan, converging from the ventral border of the episternum, from the pleural ridge, and from the tendinous lateral insertion of pv_7 to a tendon inserting (with pd_{2a}) on the 3d axillary sclerite.
- pd_3 Plates 7, 14. A thin, broad fan converging from the ventral margin of the episternum to a tendon inserting on the ventral margin of the 1st axillary sclerite, and (in some specimens at least) with one or a few fibers going to the 3d axillary sclerite near its articulation with the posterior notal process.

Pleuroventral muscles

- pv_1 Plates 6, 7, 13, 14. A thin, narrow band converging from a groove in the prepectus to a tendon inserting on the ventromedial margin of the basalare.
- pv_2 Plates 6, 7, 13. A thick band from the dorsal surface of the basicosta to the anterior margin of the basalare, inserting with and just anterior to the basalar fibers of pv_3 .
- pv_3 Plates 7, 12, 13. A thin bundle from the basalare to the median (depressor) tendon of the trochanter, joining dv_3 .
- $pv_{4(5)}$ Plates 6, 14, 15, 16. A broad, thick muscle, not obviously subdivided (as pv_4 and pv_5 in *Telea*) from the ventral portion of the meron to the subalare.
- pv_6 Plates 8, 14. A thin fan converging from the episternum anterior to the pleural ridge to the anterodorsal margin of the coxa.

- pv₇ Plates 7, 8, 14, 15. A flat, narrow, ligamentous band from the ventral portion of the pleural ridge to the base of the posterior furcal arm. Muscular chiefly at its furcal end, and withstanding treatment with KOH.

Sternopedal muscles

- st₁ Plates 10, 12. A broad, short fan converging sharply from the ventral median plate of the sternum to the anteromedial angle of the coxa just anteroventral to the insertion of *dv*₂.
- st₂ Plates 8, 10, 12. A broad fan from the anterior part of the median ridge of the furca to the median (depressor) tendon of the trochanter.
- st₃ Plates 7, 8, 10, 12. A small bundle from the median ridge of the furca to the posteroventral portion of the merocosta.
- st₄ Plates 7, 8, 13. A thin, broad fan diverging from the median ridge of the furca laterally to the merocosta. Absent in *Telea* according to Nüesch.

Coxal muscles

- cx₁ Plates 7, 8, 12, 13. A broad, spoonlike fan converging from the anterior and medial surfaces of the basicosta to a tendon inserting on the anterior lip of the trochanteral groove.
- cx₂ Plates 13, 14. A thick, funnel-shaped muscle converging from beneath the lateral portion of the basicosta to a tendon plate in the lateral articular membrane of the trochanter, which it elevates.
- cx₃ Plates 6, 7, 8, 12, 13. A short, conical muscle converging from the posteromedial portion of the basicosta to a tendon inserting near the base of a tubercle on the posteromedial edge of the trochanter, which it elevates.

Spiracular muscles

- sd Not found in *Crymodes*.
- so Plate 8. A small bundle from the postcoxal bridge of the mesothorax to the ventral border of the anterior lip of the spiracle.

MESOTHORACIC AND ABDOMINAL MUSCLES

- IIdl₁ Plate 10. The median longitudinal dorsal muscle of the mesothorax.

- IIv1_{1a} Plates 8, 10, 12. Band from the mesothoracic furca to the anterolateral margin of the anterior furcal arm of the metathorax.
- IIv1_{1b} Plates 10, 12. Narrow band from the mesothoracic furca to the anteromedial margin of the anterior furcal arm of the metathorax.
- IIp₂ Plates 7, 8, 12, 14, 15. A pleural, intersegmental muscle. A short, subconical bundle converging from a boat-shaped tendon plate which articulates freely by a short, stemlike tendon attached to the mesothoracic postalar bridge, to the anterior surface of the pleural wing process.
- IIis Plates 8, 12. An intersegmental muscle consisting of two distinct bundles which arise on the mesothoracic furca and converge to join the tendon of *pv*₂, inserting with the latter on the basalare. (See Nüesch, 1957, footnote 1, p. 624.)
- Idl₁ Plates 6, 10, 12. The external median longitudinal dorsal muscle of the first abdominal segment.
- Idl₂ Plate 6. A narrow band from the base of the hood just lateral to *idl*₃ to the posterior end of the tergopleural suture.
- Idl₃ Plates 6, 7, 10, 12. A gently diverging bundle arising near the base of the hood on the dorsal surface of pocket II and passing by a slim tendon beneath the tergopleural suture to the antecosta of the second abdominal segment near its midpoint. Homology to *IIIIdl*₃ is not suggested.
- Idv_{ab} Plate 6. Two divergent bands from the lateral margins of the first abdominal furca to insertions respectively on and just posterior to the caudal lip of the tergopleural suture.

Table I provides a ready means of comparing the metathoracic (and intersegmental) muscles of *Crymodes devastator* with those of certain other Lepidoptera as described by various writers. Here the muscles are arranged according to the scheme employed by Snodgrass (1935). Homologies of several are doubtful, particularly those of the axillaries. Muscles such as the tergopleurals, which were found in *Crymodes*, are not listed for the other species even though they may occur in some. The syntomid *Amata lucerna* was chosen for reference from among the various Lepidoptera figured by Maki because it is the only one of his species which has a thoracic tympanum.

DISCUSSION

In a comparison of the metathoracic muscles of *Crymodes* with those of *Telea*, the similarities are more impressive than the differ-

TABLE I.—*Metathoracic muscles of several Lepidoptera as described by various writers, tabulated in order of Snodgrass's classification (1935)*

	Snodgrass (1935)	Sphinx Berlese (1909)	Papilio Weber (1928)	Amata Maki (1938)	Telega Nitsch (1953)	Crymodes
A. Dorsal						
mA	37	37	...	54	dl _{1a} , b	dl _{1a} , b
1A	38	38	...	55	dl ₂	dl ₂
B. Tergopleural						
C. Tergosternal	XXXVI	XXXVI	III dvm ₁	57	dv ₁	dv ₁
D. Axillary						
" "	? III pm ₃	? 62	? pd ₃	pd ₃
" "	? III pm ₃	? 62	pd _{2a}	pd _{2a}
" "	III pm ₆
" "	56a	56a	III pm ₆	61	pd _{2b}	pd _{2b}
" "	56	56	III pm ₆	62	pd _{2c}	pd _{2c}
E. Epipleural						
2E'	64	pv ₁	pv ₁
3E'	XLVII	XLVII	III pm ₁	72	pv ₂	pv ₂
F. Lateral intersegmental	XLIX	XLIX	III pm ₁ , 5	69	pv ₄ , 5	pv ₄₍₆₎
" "	73a	73a	...	63	II pv ₈	IIIs
" "	(= IIIs,	
" "	1957)	
" "	II p ₂	II p ₂
G. Pleurosternal						
H. Ventral	65	65	III vlm ₁	85	dv ₇	dv ₇
" "	36	36	III vlm ₁	80	v ₁	v ₁
" "	68	68	II vlm ₁	81	v ₂	v ₂
" "	(quarto)	(quarto)	II vlm ₁	56	II v _{1a}	II v _{1a}
" "	68	68	II vlm ₂	57	II v _{1b}	II v _{1b}
" "	(quinto)	(quinto)	III dvm ₂	66	dv ₂	dv ₂
I. Tergal promotor of leg.	42	42	III dvm ₂	68	dv ₄ , 5	dv ₄₍₆₎
J. Tergal remotor of leg.	43	43	III dvm ₄	67	st ₁	st ₁
K. Sternal promotor of leg.	III bm ₁	70	st ₁ (?st ₁)	st ₁ (?st ₁)
L. Sternal remotor of leg.	III bm ₃	70	st ₁	st ₁
M. Pleurocoxal	51	51	III pm ₇	71	pv ₆	pv ₆
N. Adductor of coxa.
O. Coxal levator of trochanter						
131	Abduttore del trochantere	Abduttore del trochantere	III cxm ₁	...	cx ₂	cx ₂
132	Abduttore del trochantere	Abduttore del trochantere	III dvm ₃	...	cx ₃	cx ₃
P. Extracoxal depressor of trochanter.	46	46	III dvm ₃	73	dv ₃	dv ₃
" "	III pm ₃	75	pv ₃	pv ₃
" "	III bm ₂	76	st ₂	st ₂
" "	III cxm ₄	...	cx ₁	cx ₁
Q. Coxal depressor of trochanter 133a.	III cxm ₄
(spiracular)	77	so	so

ences, and this notwithstanding the presence of the tympanum in the noctuid and its absence in the saturniid. No single feature of the noctuid musculature appears to be uniquely associated with the tympanic organ. Each of the muscles of the tympanic region has its counterpart in *Telea*, and there seems no reason to suppose that the function of any of them is drastically different in the two insects. Muscle dl_{1b} (Eggers's median muscle) is so situated that its contraction could have but little if any effect upon the tympanic air sac. More than likely it is a functionally unimportant vestige of a longitudinal flight muscle. Muscle dl_{1a} (Eggers's separate fan-shaped bundle of the median muscle) might be capable of expanding the air sac by direct action, though this effect would presuppose a firmer origin than the prescutum appears to afford. Muscle dl_2 (Eggers's middle muscle, *mM*) runs almost tangent to the air sac from the scutum to the anterior tendon plate (*Muskelleiste* of Eggers), which seems braced to resist displacement in this direction. There is nothing to suggest that this muscle could affect the tension of the tympanic membrane, and in any event it has been shown (Roeder and Treat, 1957) that tension in this structure is not essential to acoustic reception. From its position, one would expect the action of dl_2 to depress the anterolateral area of the scutum and thus to aid in elevating the wing. Muscle $dv_{4(5)}$ (Eggers's lateral muscle) could scarcely affect the tympanic region in any way; it is probably effective in elevating the wing and is classed as a tergal remotor of the coxa. Muscle $pv_{4(5)}$, by virtue of its insertion on the subalare, might compress the lateral end of the tympanic air sac indirectly as an incidental consequence of wing movements. Snodgrass (1935, p. 206) describes this muscle in the adult *Dissosteira* as a depressor-extensor of the hind wing; it may well have a similar action in *Crymodes*, though its effect on the tympanic air sac is hard to evaluate. It is noteworthy that the metascutum is divided into anterior and posterior portions along a hingelike line which follows the base of the scutal phragma. The anterior portion, to which most of the vertical flight muscles are attached, can thus be depressed without marked displacement of the posterior part which roofs the tympanic air sac.

Eggers thought that the structure of the tympanic organ was such as to resist the deforming stresses that might result from muscular activity.³ Detailed consideration of the metathoracic muscles tends to

³ "Einigermassen fixiert ist die Form der Blase durch zwei kräftige, nach innen gebogene Chitinleisten, die sie erfassen und einer Zerrung und Deformierung durch die Tätigkeit der Muskulatur entgegenwirken."—Eggers, 1919,

reinforce this conclusion. There is no suggestion of a "tensor tympani" effect nor of a device such as that postulated by Hinton (1955) for the reduction of acoustic sensitivity during some part of the wing-beat cycle. The fact (Roeder and Treat, 1957) that the tympanic membrane can be widely perforated without materially affecting the acoustic response as recorded from the tympanic nerve, suggests that a mechanism for reducing the tension in that membrane would have but little physiological effect upon the sense of hearing. Yet it cannot be stated categorically that no such mechanism exists. The regular pattern of impulses recorded from the Bügel cell, and the modification of this pattern by the stretching of the Bügel sheath must tempt speculation in such directions even in the absence of confirmatory evidence. No one can give close attention to the anatomy of the noctuid metathorax without realizing the baffling architectural subtlety of the tympanic organ. It would be rash indeed to attempt conclusions as to function from the morphological consideration of so intricate a structure.

ABBREVIATIONS USED ON FIGURES

Segmental structures are those of the metathorax except where otherwise indicated. A roman numeral preceding an abbreviated name refers to a thoracic segment. An arabic number 1 preceding an abbreviated name refers to the first abdominal segment except for the axillary sclerites of the metathoracic wing which are designed as 1Ax, 2Ax, and 3Ax respectively. Names of muscles are abbreviated in lower-case letters, those of other structures, with initial capitals. Terminology follows mainly that of Nüesch (1953 and 1957).

<i>AbF</i> , abdominal furca.	<i>BF</i> , base of furca.
<i>AF</i> , anterior furcal arm.	<i>Bst</i> , basisternum.
<i>Al</i> , alula.	
<i>ANP</i> , anterior notal process.	<i>CA2-3</i> , connective from abdominal ganglion 2 to 3.
<i>Ao</i> , aorta.	<i>Cj</i> , conjunctiva.
<i>ATP</i> , anterior tendon plate.	<i>CTC</i> , countertympanic cavity.
<i>Ax</i> , axillary sclerite (see 1, 2, 3Ax).	<i>CTM</i> , countertympanic membrane.
<i>A1 + 2</i> , abdominal ganglia 1 and 2.	<i>CTMO</i> , orifice resulting from removal of countertympanic membrane.
<i>B</i> , Bügel.	
<i>Ba</i> , basalare.	

p. 303. The two structures referred to by Eggers are the scutal phragma (*Spannleiste*) and the anterior tendon plate (*Muskelleiste*). To these might be added the dorsomedial sclerotization of the tympanic air sac, to which the fibers of muscle *dh_a* are attached. The ventral margin of this sclerotization appears in plate 2 as an upcurved line (unlabeled) from near the base of the anterior tendon plate and passing between the labels *B* and *Ep*. The structure, which has never been adequately described, seems to be a phragmatal ingrowth from the posterior and medial borders of the countertympanic frame, and would thus be postnotal in origin.

- CTO*, external orifice of countertympanic cavity.
CTS, countertympanic septum.
Cx, coxa.
cx, coxal muscle.

dl, dorsolongitudinal muscle.
DLT, deep lateral thoraco-abdominal tracheal trunk.
dv, dorsoventral muscle.

Ep, epaulette (nodular sclerite).
Epm, epimeron.
Eps, episternum.

G, ganglion.
Gt, gut.

H, hood.

IM, intersegmental membrane.
is, intersegmental muscle.

L, ligament.
LG, labial (salivary) gland.

M, meron.
MAS, median air sac.
Mc, merocosta.
MRF, median ridge of furca.
Msph, mesophragma.

N, nerve.
nM, median nerve.

p, pleural muscle.
PI, pocket I (epimeral).
PII, pocket II (postnotal).

PIII, pocket III (postnotal).
PIV, pocket IV (epimeral).
PcB, postcoxal bridge.
pd, pleurodorsal muscle.
PF, posterior arm of furca.
PIR, pleural ridge.
PNP, posterior notal process.
PO, pulsatile organ.
Pp, prepectus.
Psc, prescutum.
PTG, pterothoracic ganglion.
PTP, posterior tendon plate.
pv, pleuroventral muscle.
PWP, pleural wing process.

S, scoloparium, containing the two tympanic sensilla.
Sa, subalare.
Sc, scutum.
Scl, scutellum.
ScP, scutal phragma.
SLT, superficial lateral thoraco-abdominal tracheal trunk.
so, spiracular occlusor muscle.
Sp, metathoracic spiracle.
Sp₁, 1st abdominal spiracle.
St, sternum.
st, sternopedal muscle.

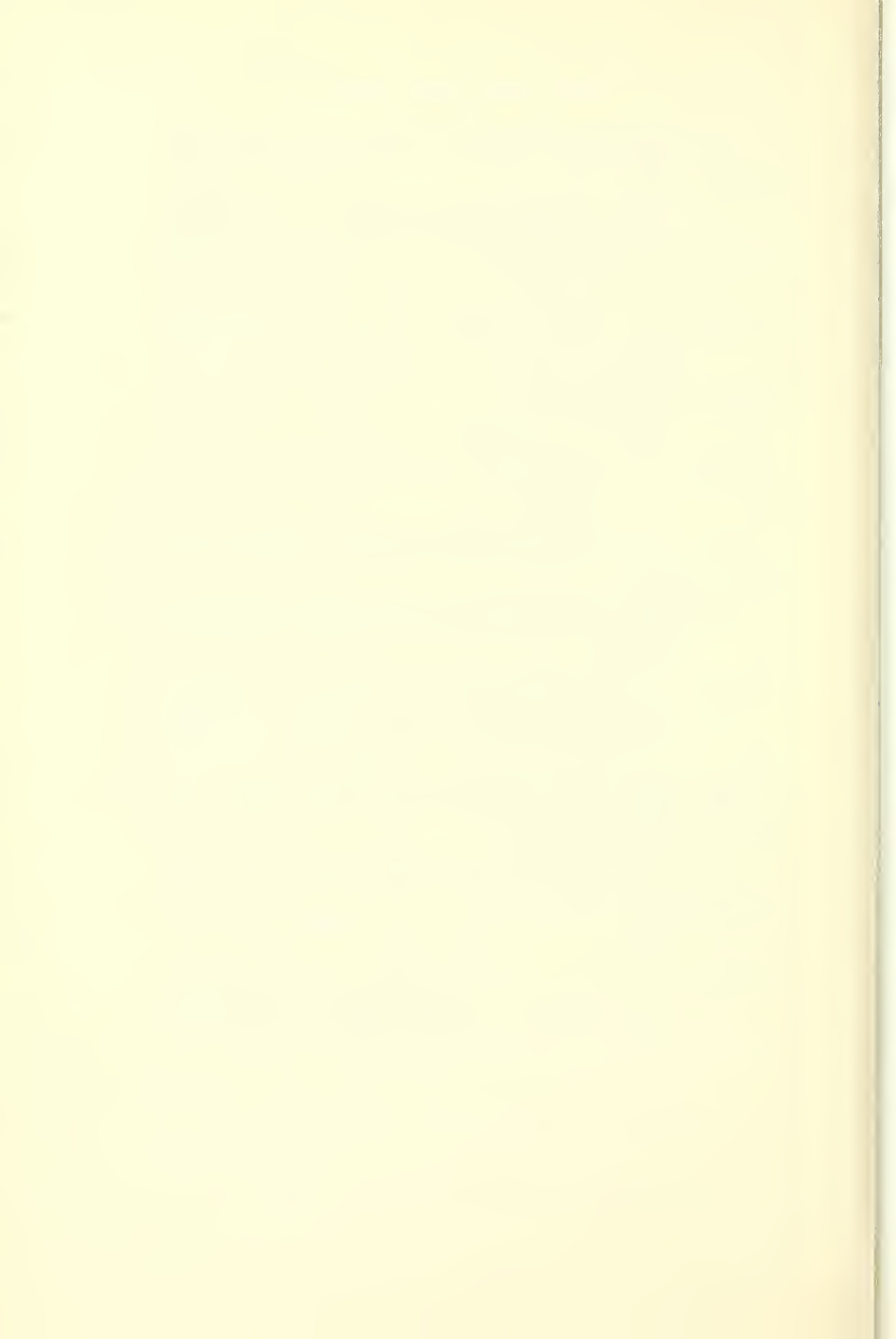
TAS, tympanic air sac.
TgA, tergal arm.
TM, tympanic membrane.
TN, tympanic twig of nerve IIIN1b.
TPG, tergopleural groove.
Tro, trochanter.

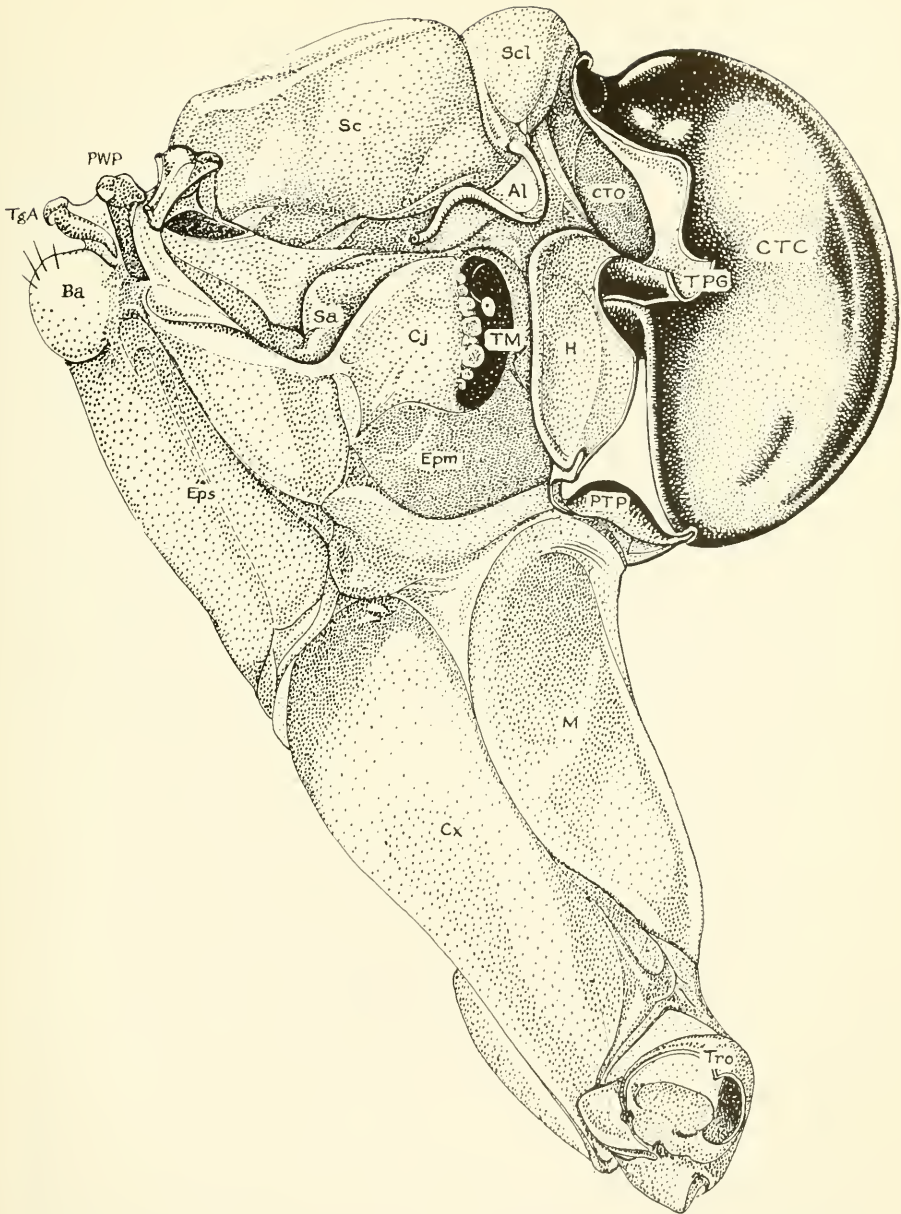
vl, ventrolongitudinal muscle.
VMP, ventral median plate of sternum.

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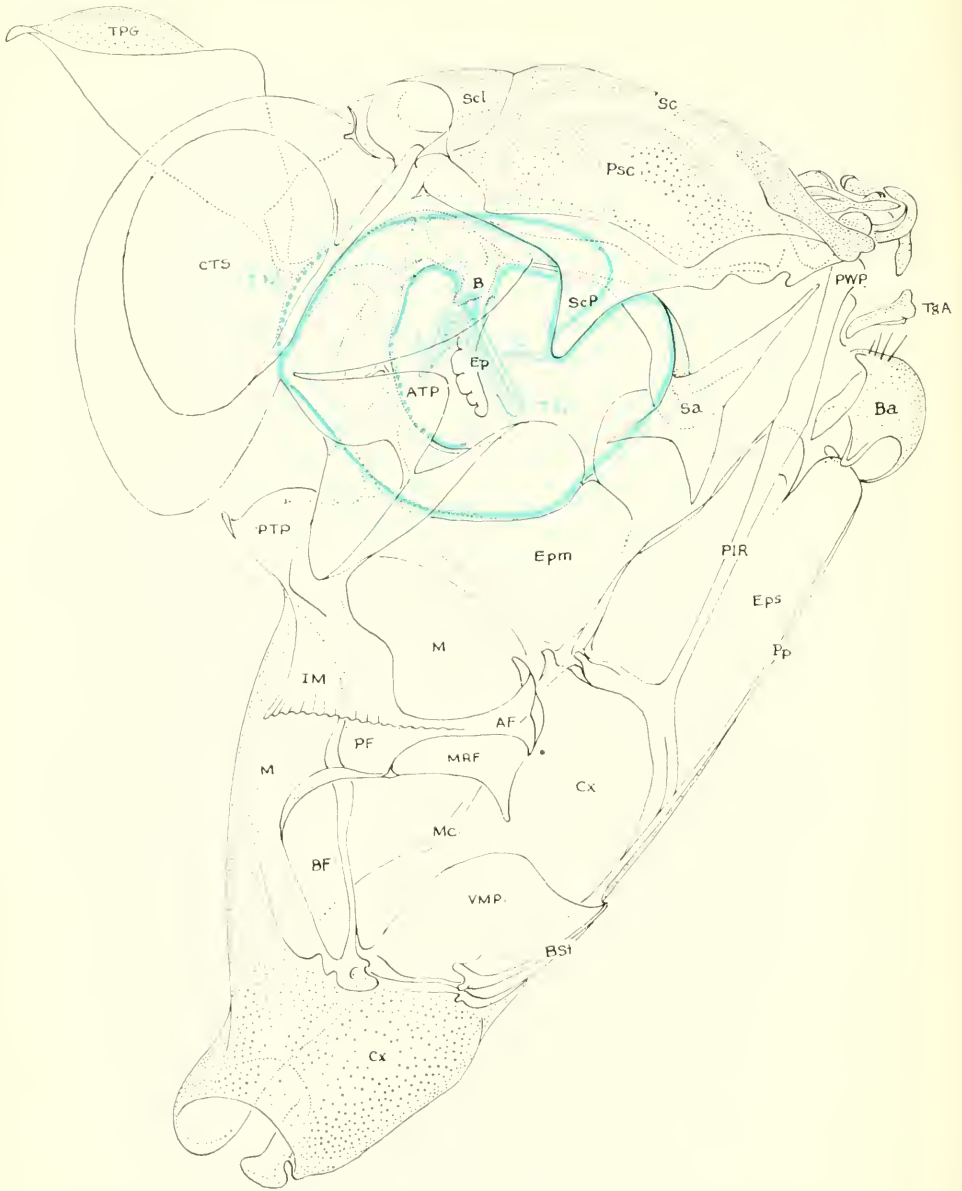
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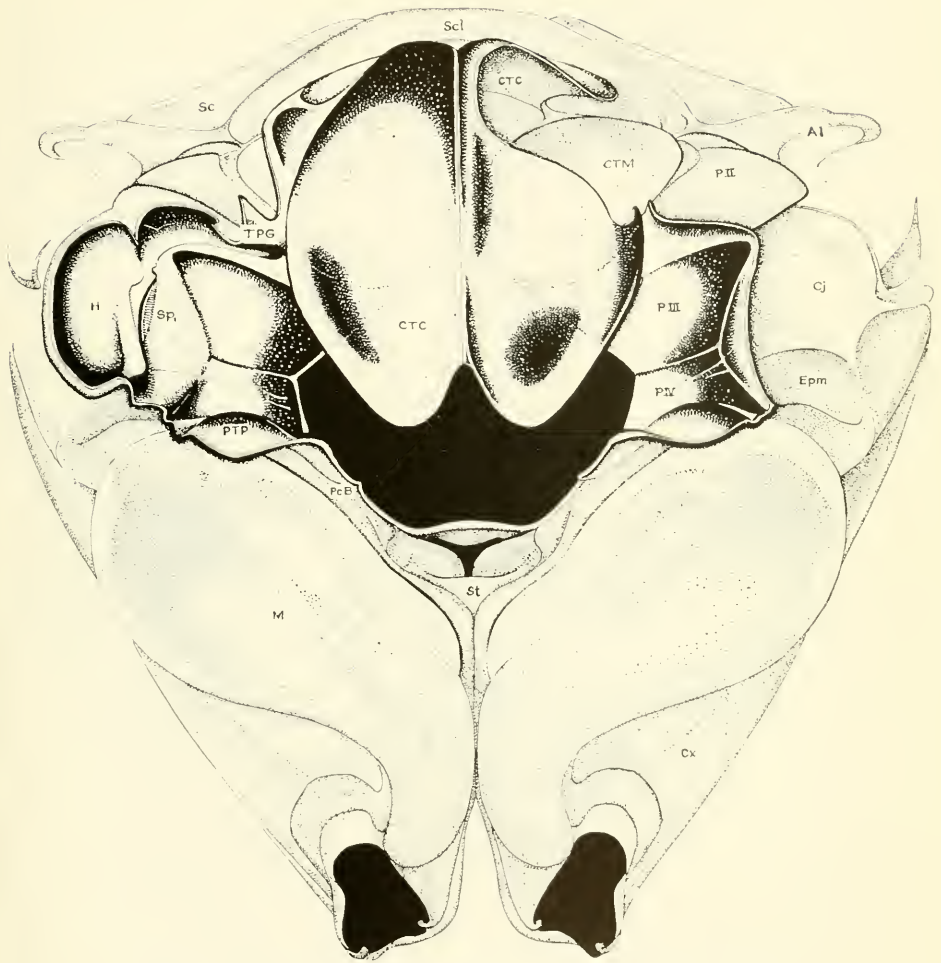




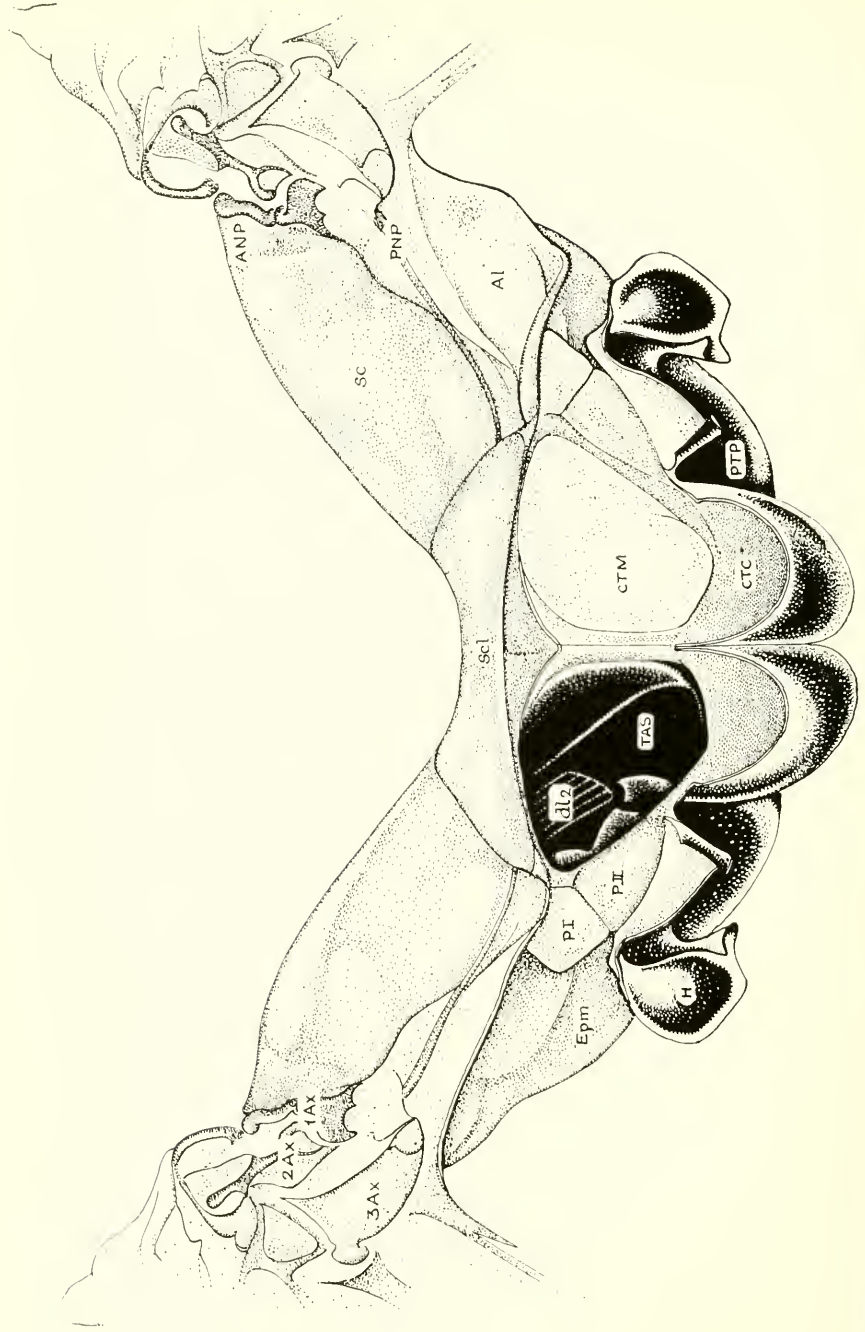
Left side of metathorax and portions of abdomen associated with the tympanum, drawn from dry, denuded specimen.



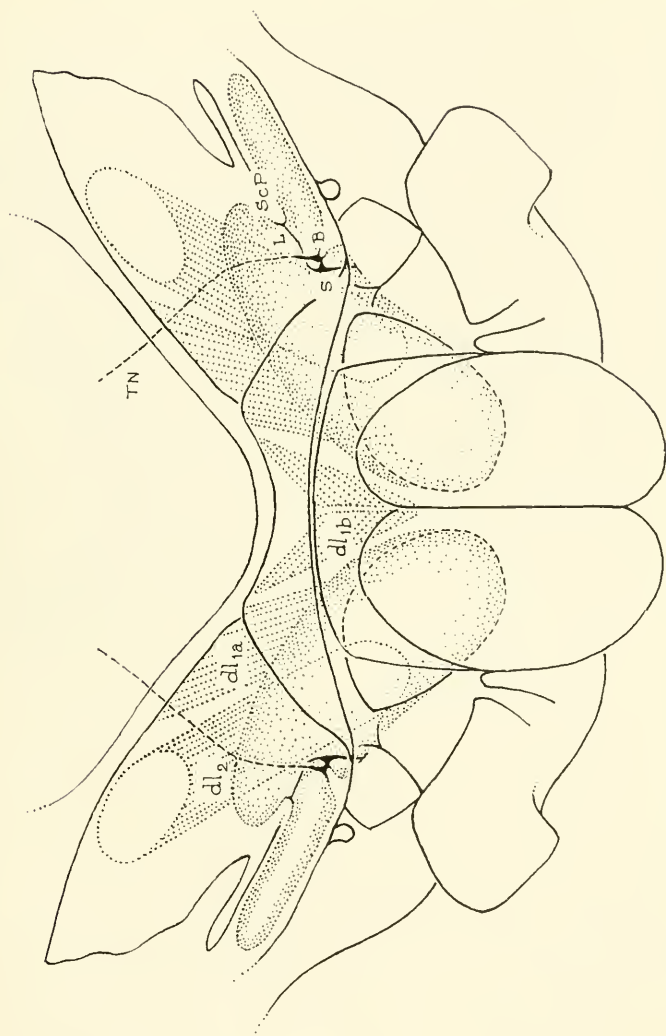
Skeletal parts of left half of metathorax and certain associated parts, median view of KOH-cleared specimen. Stippling indicates exterior surface; dotted lines, structures seen through transparent overlying parts. Color overlay shows outline of tympanic air sac with nervous elements and epithelial sheaths of Bügel, scoloparium, etc., in blue.



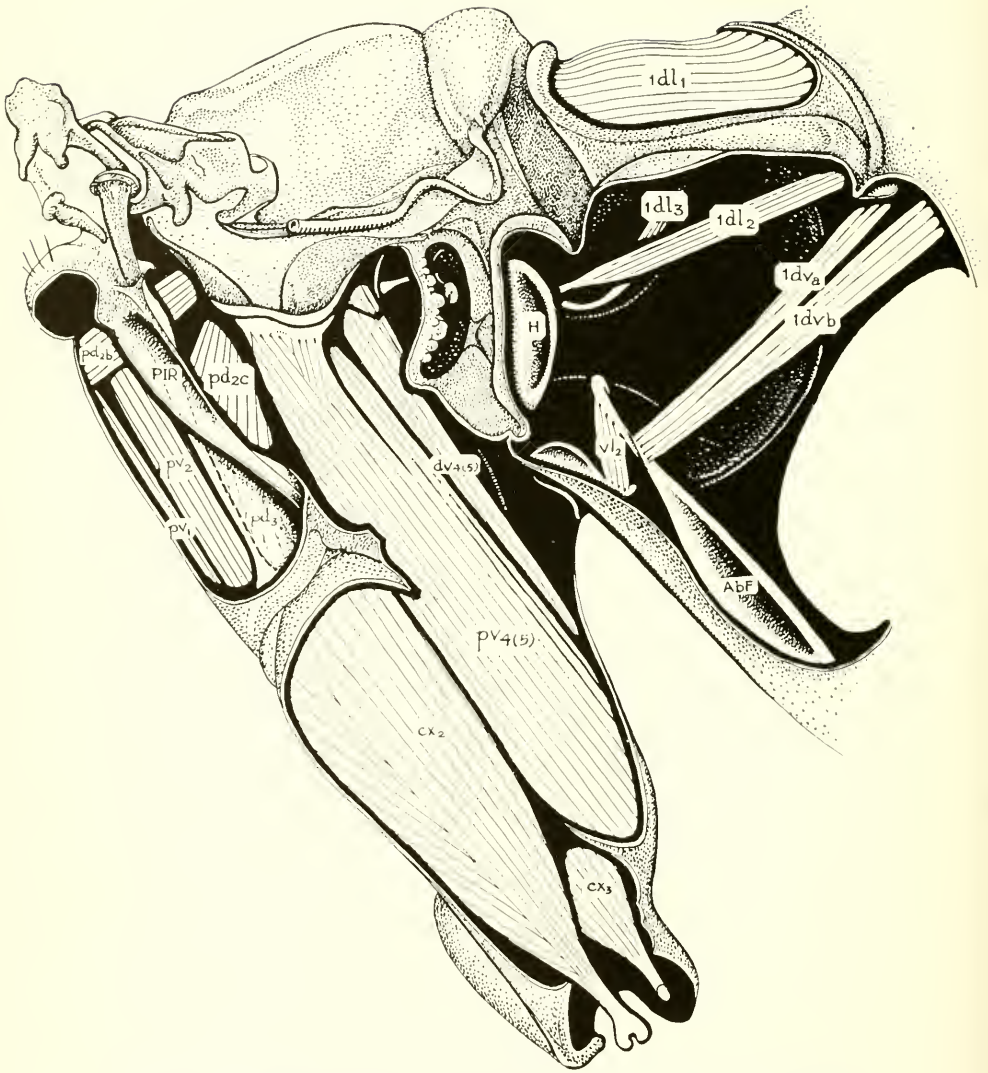
Posterior view of dry, denuded metathorax after removal of abdomen.



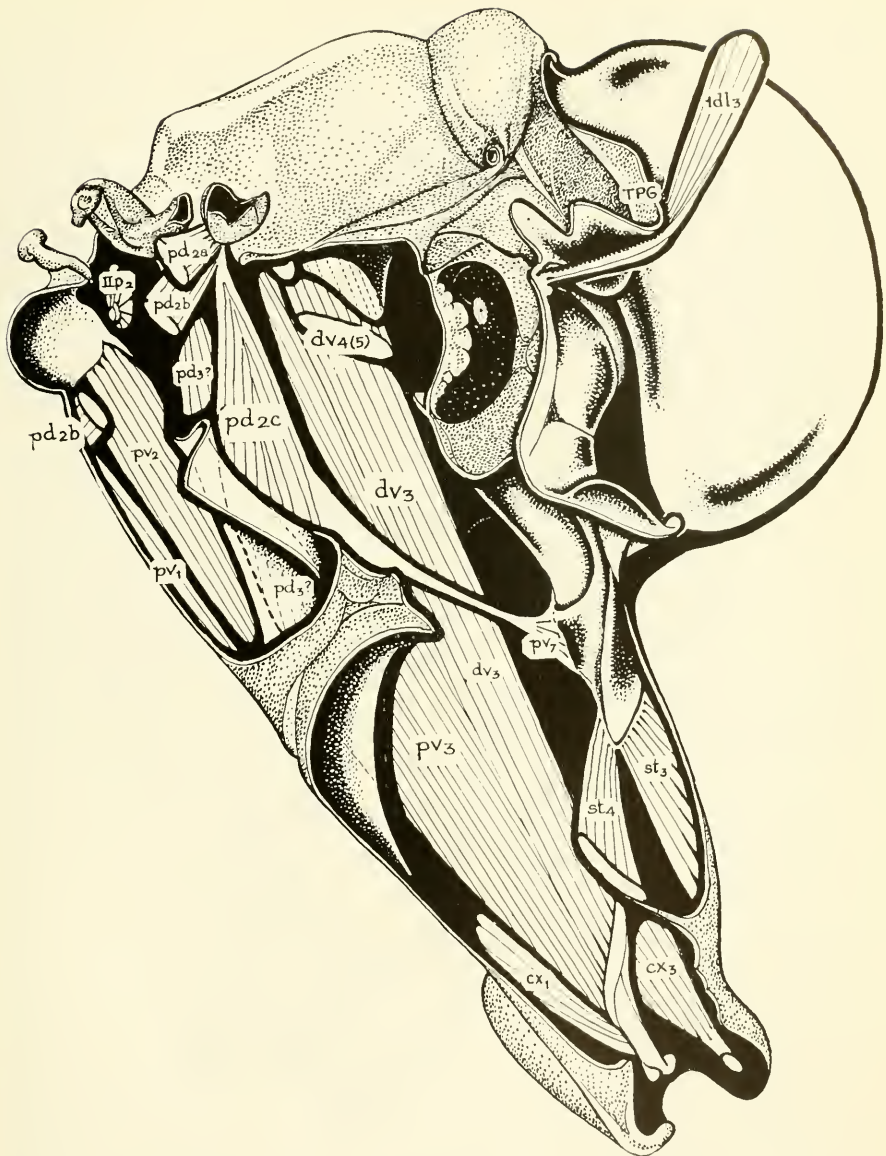
Dorsal view of dry, denuded metathorax and certain associated parts after removal of left countertympanic membrane. Compare plate 5.



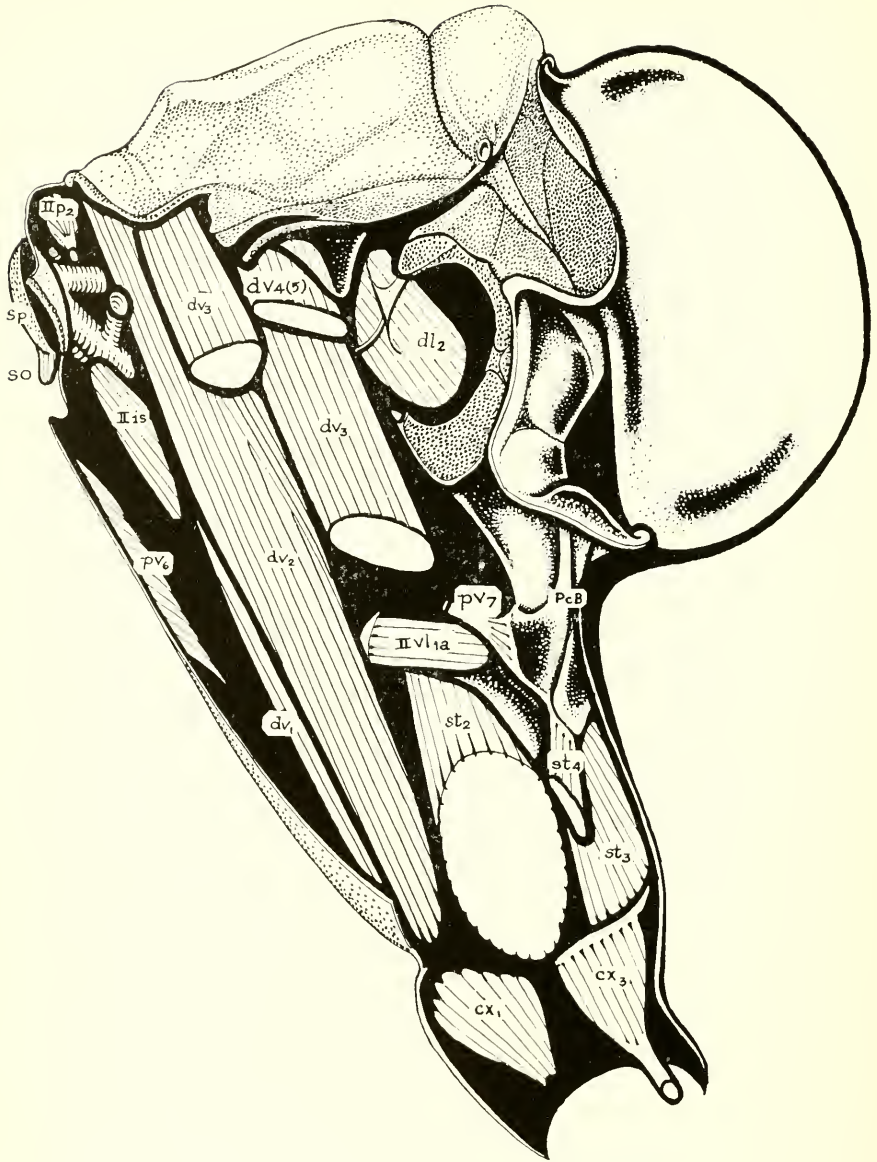
Schematic stereogram of metathorax as seen from above, to show relation of tympanic structures to certain skeletal and muscular features. The tympanic air sac is shown by stippled shading. See plate 4 for skeletal parts.



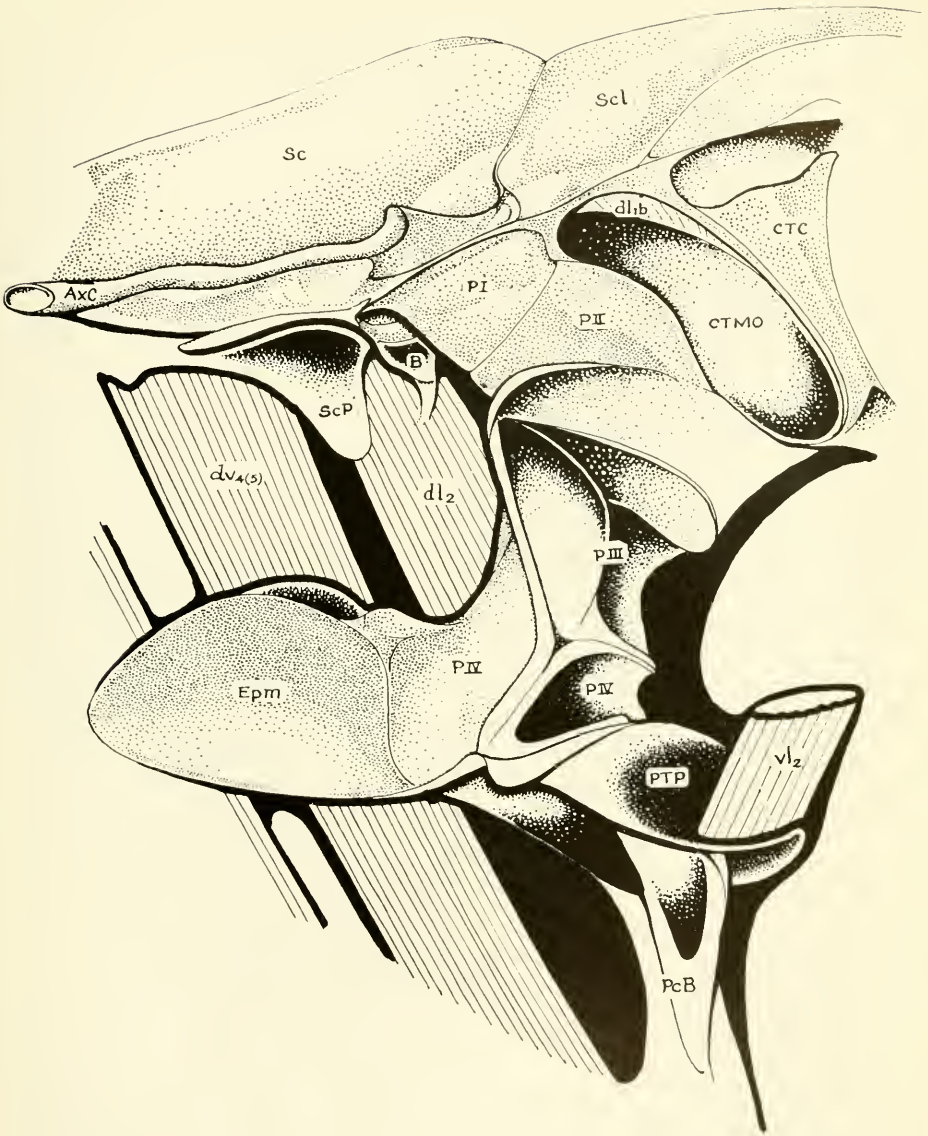
Superficial muscles of metathorax and first abdominal segment, left side view.



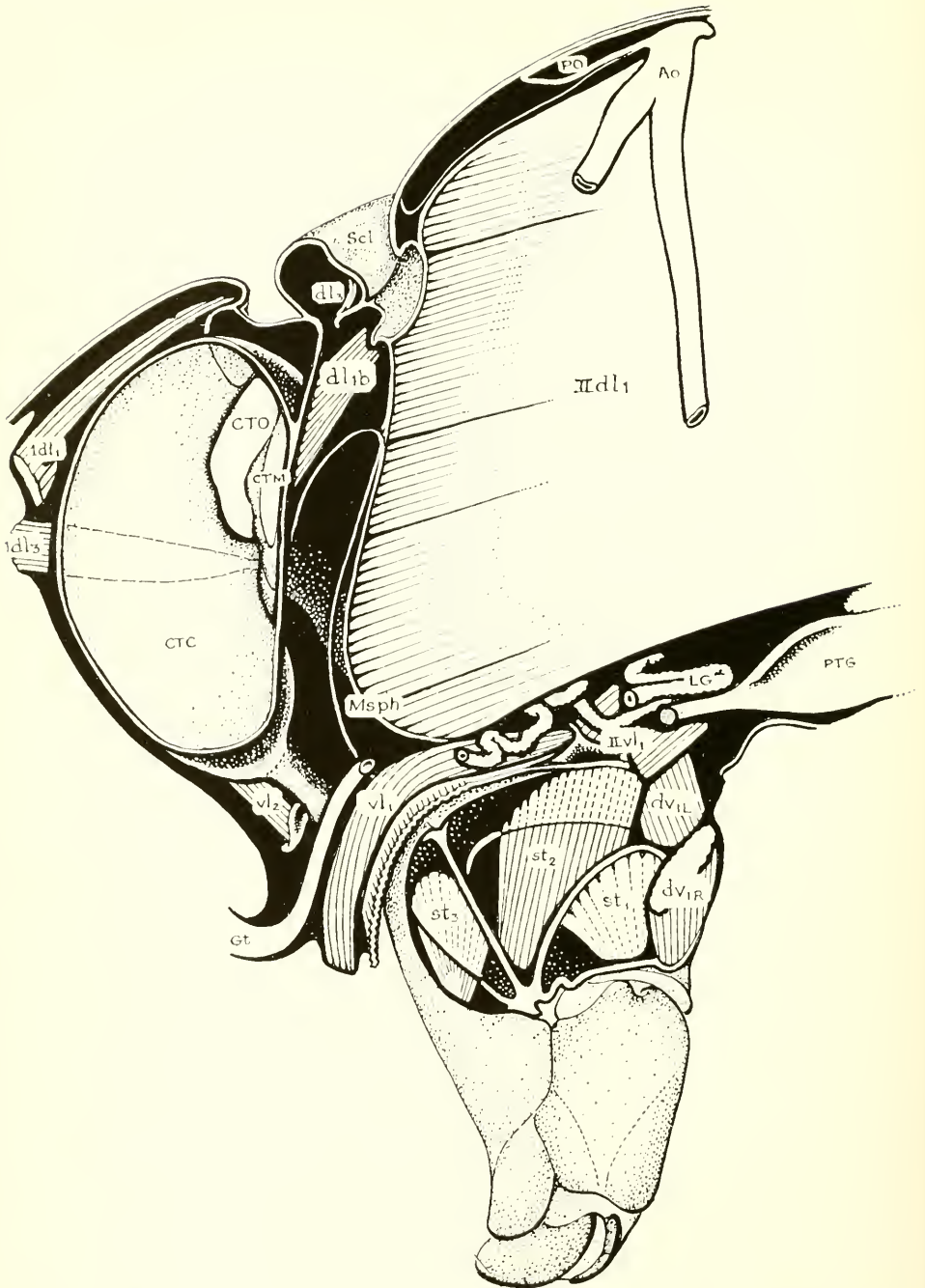
Left side of metathorax after removal of certain superficial muscles.



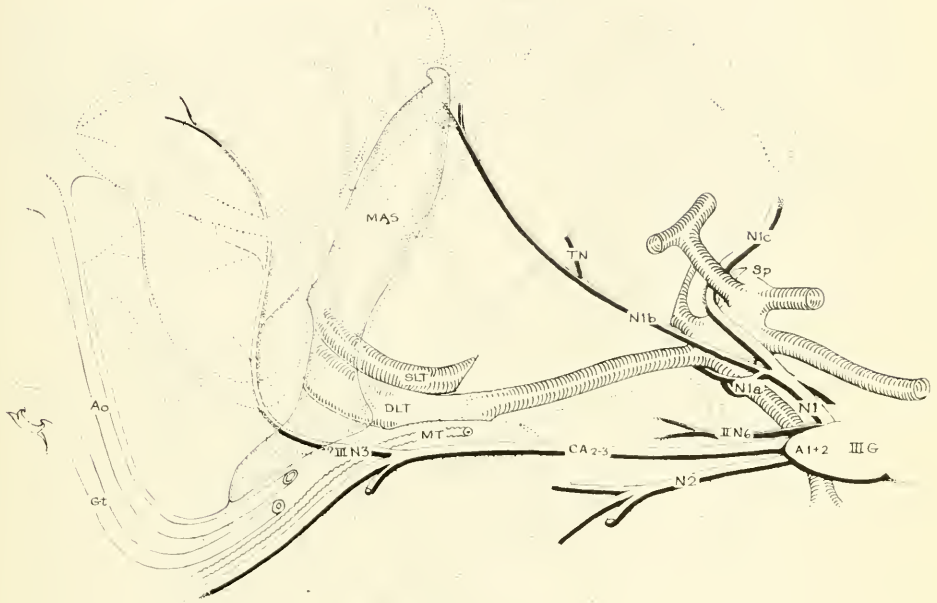
Left side of metathorax showing deeper muscles.



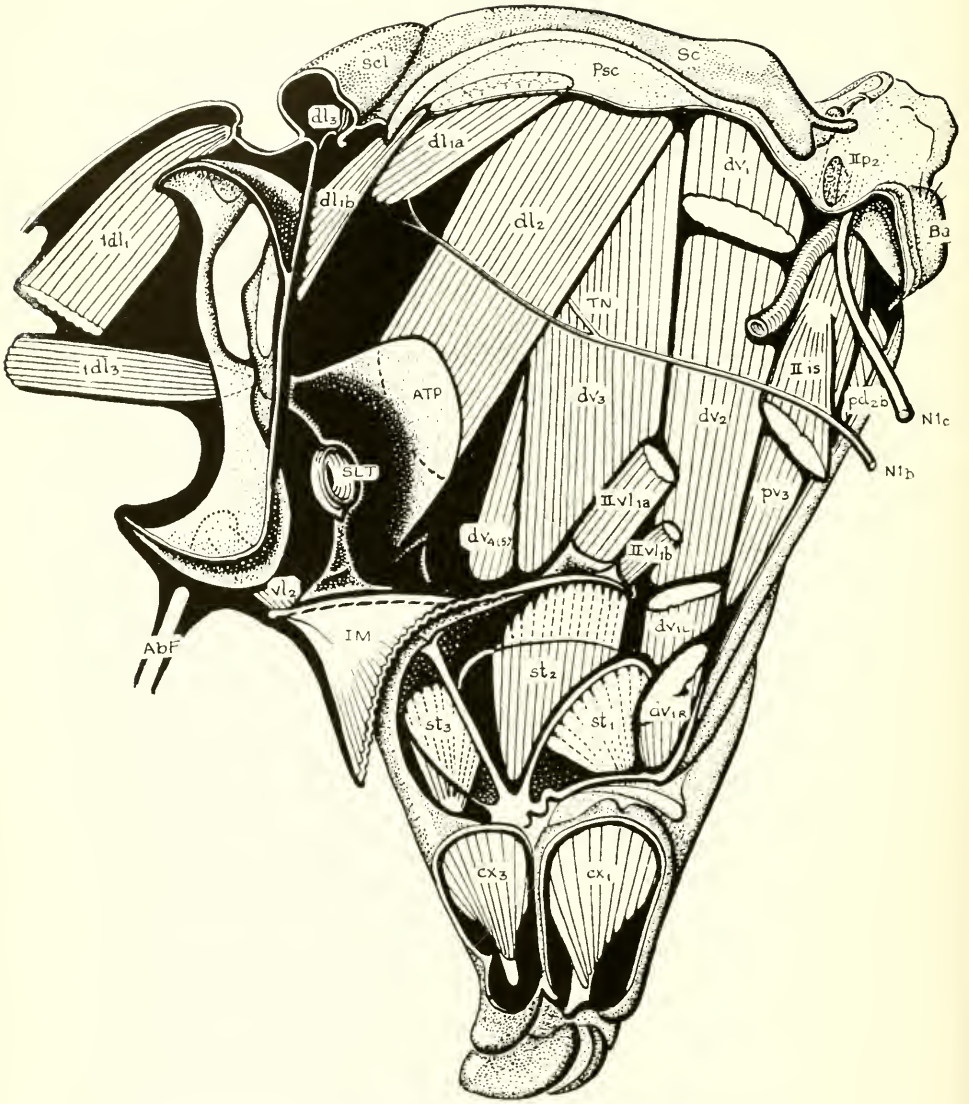
Left tympanic frame and associated structures after removal of tympanic and countertympanic membranes and posterior walls of pockets III and IV.



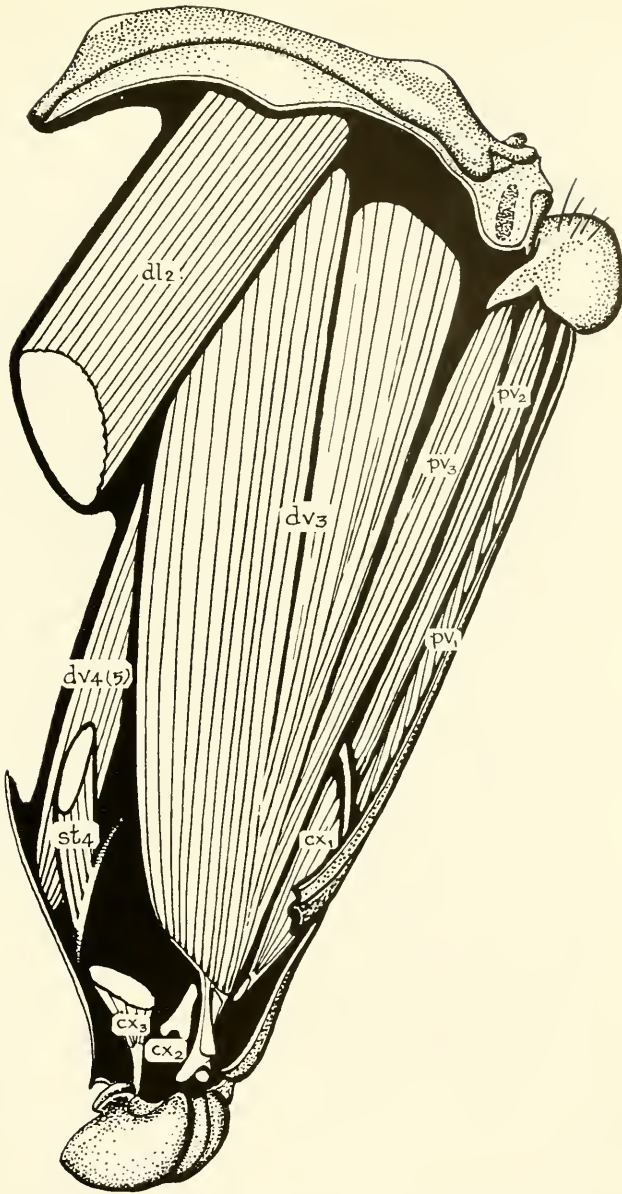
Median view of left half of metathorax and parts of mesothorax and first abdominal segment, undisturbed after hemisection.



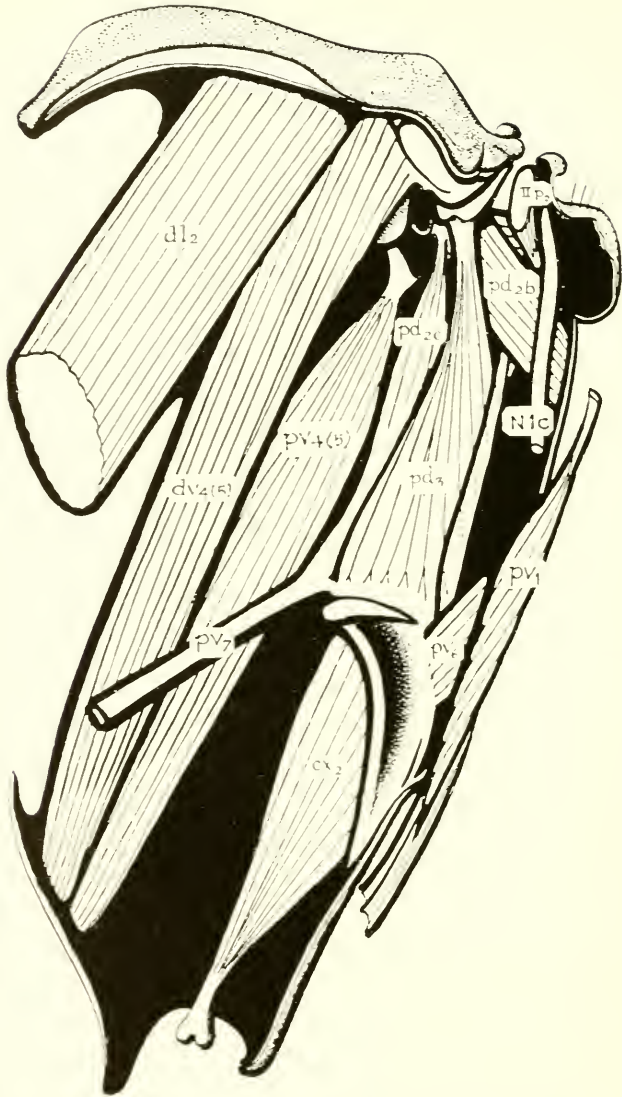
Schematic view of main metathoracic tracheal and nerve trunks as seen in median view after removal of mesophragma and muscle *II d1*.



Deep muscles of metathorax, median view after partial dissection.



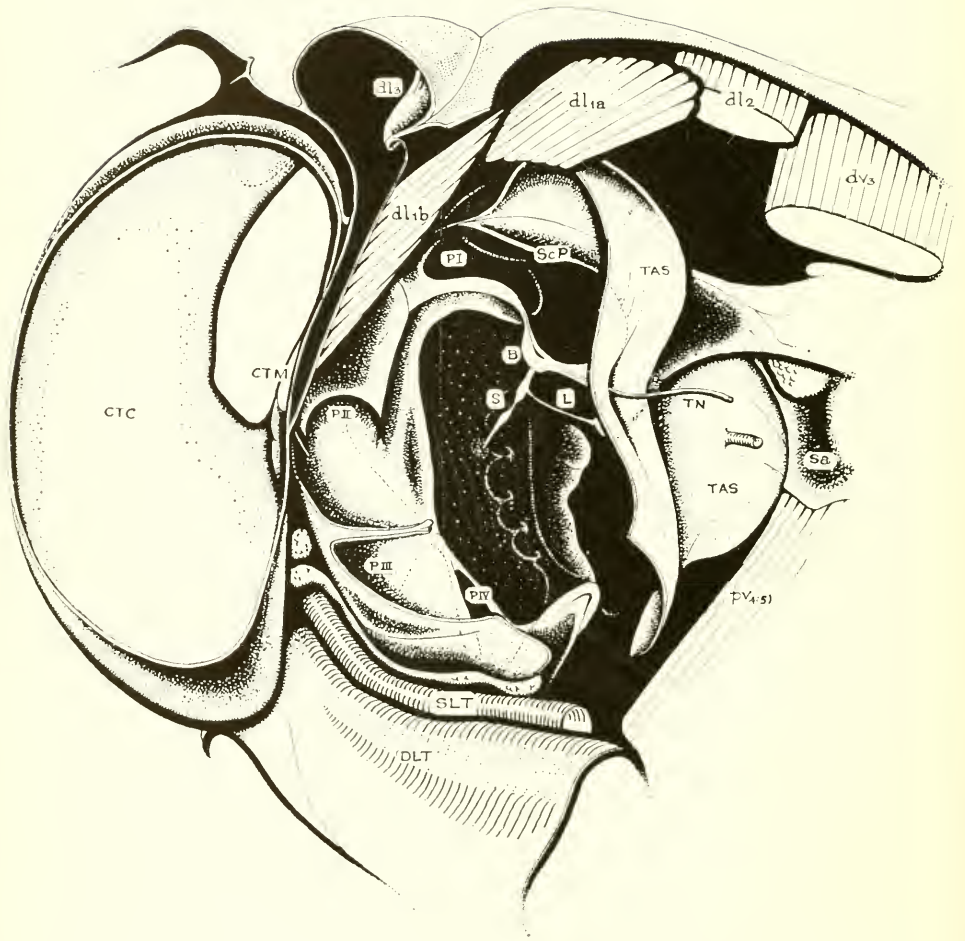
Median view of metathorax after further dissection and removal of *dl1*, *dl2*, and certain other deep muscles.



Superficial muscles, median view after still further dissection.



Detail showing certain muscles of the wing articulation, median view.



Left tympanum and associated structures, median (internal) view after opening of the tympanic air sac and partial dissection.

THE PHYLOGENETIC SIGNIFICANCE OF ENTOGNATHY IN ENTOGNATHOUS APTERYGOTES

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In recent years more and more voices are raised in support of a separation of entognathous apterygotes from the ectognathous ones, of removing the entognathous ones from the class Insecta, and even of removing them very far from each other. Thus, Handschin in 1952 urged that the Collembola should be made a class of its own—Protomorpha. Remington in 1954 summarized what was to be said on this matter in a clear and scholarly paper and gave his own opinion to the effect that "Myriapoda" and Insecta might be grouped as a subphylum Insecta subdivided in sections, superclasses, and classes as follows:

Subphylum Insecta

Section Myocerata

Superclass Dignatha

Class Pauropoda

Class Diplopoda

Superclass Trignatha

Class Chilopoda

Class Labiata

Order Collembola

Order Protura

Order Symphyla

Order Entotrophi (= Diplura)

Section Amyocerata

Class Thysanura

Class Pterygota

Subclass Paleoptera

Subclass Neoptera

Pactl, on the other hand, in a discussion with Hennig (1954 and 1956a) and in his compilatory work of 1956(b) concluded that winglessness among what he (as well as Remington) calls primitively wingless insects (also adopted by Sharov in his papers on Thysanura and Monura) is a monophyletic character, all apterygotes being one group, at the base of Insecta.

Obviously, it is a purely verbal problem whether or not to call the

entognathous apterygotes Insecta—a verbal and a technical problem: must they be mentioned in entomological textbooks? The common concept of an insect among laymen is that they are creatures with six legs; and the few instances of other arthropods with six legs (among Acari and young myriopods), of course, do not alter this. So the layman and the student will look for the three groups of entognathous apterygotes in entomological handbooks, and they should not be disappointed. The theoretical problem of the relationship of entognathous apterygotes is, however, of much more interest; Remington made a fine survey of the characters uniting or distinguishing the groups of myriapods and insects. One of these characters I have always found of very great importance, namely, the entognathy itself in the three orders Protura, Collembola, and Diplura, because if it is true that Collembola and Protura, far away from each other, branch off at a “low” place on the “tree” of arthropods, and Diplura much higher up, together with Symphyla, nearer the true insects, it means that the character entognathy is polyphyletic. Remington (1954, p. 499) puts it thus: “The phylogenetic significance of this condition is obscure, but there seem to be excellent reasons for regarding its origin as independent in each of these three groups.”

What I wish to do in the following pages is to look a little deeper into this question through a comparative analysis of the entognathy in the three groups. I might have done it better by making sections, which circumstances did not permit at the time, or by using a finer technique; I hope, however, to present a survey which may furnish us with the means for a clearer insight.

As to the technique, I shall mention only that I have treated the insects (if I may be allowed to use this word) with lactic acid for a shorter or longer time at different temperatures. Treatment for 24 hours at 55° C. will clear them up a little, at 80° C. much more, and in both cases the muscles will remain, most visible in the latter case, when, however, the mesodermal “tentorium” will be more or less dissolved. Boiling the insects for only a few minutes in lactic acid will clear them of all mesodermal tissue and leave the chitin untouched even in its finest strands. By combining views of heads treated in these ways, the accompanying figures were made. No staining was used. All slides used for the drawings are kept in the Zoological Museum of Copenhagen, so that the results can be checked at any time.

Now, the basic question of course will be: how is entognathy to be understood? On this point Denis (1949, p. 112) writes: “L’entognathie ne résulte pas de l’enfoncement des gnathes mais de leur re-

couvrement par un 'pli oral' des g nas et postg nas, r unissant clyp us et labium et s' tendant, comme un volet, au-dessus des mandibules et maxilles. . . . Le pli oral d rive d'anciens  pipodites subcoxaux."

Snodgrass (1952, p. 271) writes: "The mandibles and maxillae are enclosed in pockets of the head formed by a union of the labium with the lateral walls of the cranium." In 1951 (p. 81) he refers this concept to the classical embryological investigation by Folsom (1900).

Pact (1956b, pp. 17-18) writes: "Bei den Collembolen und Proturen beschr nkt sich die Mund ffnung auf den rein frontalen Teil des Kopfes, weshalb die hier tiefer versenkten Mundgliedmassen dauernd in der Mundh hle versteckt bleiben und von den Seiten nicht sichtbar sind. Gerade entgegengesetzte Verh ltnisse beobachtet man bei den Dipluren, wo die frontolaterale Lage der Mund ffnung es dem Tier erm glicht, die Mundgliedmassen teilweise nach aussen hin auszusetzen. Da aber auch die Mundteile der Dipluren in die betreffende Einst lpung des Kopfes tief versenkt sind, werden die Collembolen, Proturen und Dipluren gemeinsam als Entognatha . . . bezeichnet."

In an attempt to form a personal opinion in this matter I have investigated many specimens of one species of each of the three groups, namely *Acerentomon doderoi* Silv. (from Birkezwischenmoor am H ftsee, Holstein, February 1941, Strenzke leg.), *Onychiurus armatus* Tullb. (from Berufj rdur, Iceland, in great numbers on the shore, July 14, 1900, A. C. Johansen leg.), and *Campodea plusiochaeta* Silv. (from Helleb k, Denmark, 1893, C. With leg.). Of course an investigation of a greater number of species would have been desirable, but time did not permit this. In the present paper the following elements will be treated comparatively in the three groups: The antennae, the entognathy, the hypopharynx and fulcrum, the mandibles, and the maxillae.

1. THE ANTENNAE

Imms in 1940 made a fine study of the antennal muscles in different groups of arthropods and arrived at the very important conclusion that the arthropod antennae were divisible into two groups, segmented antennae and annulated antennae, the first group having intrinsic muscles in all segments, the second possessing intrinsic muscles only in the pedicel, consisting of from one to four segments, the rest of the antenna lacking independent movement. Segmented antennae were found in all groups known as Myriapoda (though a transitional

form occurs in the Schizotarsia), in the lower Entomostraca such as Copepoda and Ostracoda, and in Collembola and Diplura. Annulated antennae are found in Malacostraca, in Thysanura (ectognathous), and in all pterygote insects. In this fact he finds—somewhat prematurely it seems to me—a support to the symphylan theory of insect descent.

Now we should want to know how the third order of entognathous apterygotes, the Protura, fits into this scheme. But the Protura have no antennae; they are the only really antennaless mandibulates, the first tarsi having taken over the function of the antennae. According to most authors the antennae have disappeared without leaving any traces. There are, it is true, some peculiar organs on the head of Protura at exactly the place where the antennae should be expected, the pseudoculi, but they are most often regarded as equivalents of the postantennal organs of collemboles, the Tömösvary organs of myriapods, and the pseudoculi of pauropods, which are all the same thing. Paclt (1956b, p. 39) even finds that they have the same function as these organs, namely, as hygrometers. He writes that "bei Anschwellung der Hypodermiszellen des Pseudoculus wird die Form des Organs nach aussen gewölbt." As he does not tell us whether the proturan was living when he made his statement, nor in fact does he give any other evidence, I suppose it to be a phenomenon of preparation and thus not convincing.

Handlirsch in 1926 supposed the pseudoculi of Protura to be antennal rudiments, and in 1931 I supported this view on the basis of Berlese's figures. I should want to emphasize it again on the basis of a preparation of the head capsule of *Acerentomon doderoi* seen from within. Figure 1 shows the pseudoculus from the ventral side and more laterally from the inside of a loosened roof of the head. The nerve to the organ and two muscles are seen, one originating from the dorsal side of the head, the other one from below the pharynx, perhaps from a mesodermal supporting structure, an endosternum (see further on in this paper). I suppose these muscles to be the antennal muscles of the organ, perhaps even able to move it, which, however, I have not had the opportunity of checking on live specimens. As no muscles, however, are found in connection with the postantennal organs of collemboles, I find in them a proof of the antennal character of the pseudoculi of Protura. And even a priori I should think it much more probable that an organ such as the antenna, present in every other mandibulate arthropod, should manifest itself as merely a rudiment, rather than the postantennal organ, lacking even in many groups of collemboles.

I have stressed this point in order to avoid separating more than necessary the three entognathous groups from each other.

2. WHAT IS ENTOGNATHY?

This problem may be approached through embryological and morphological investigations.

The embryology of *Campodea "staphylinus" Westw.* (Diplura) was studied by Uzel (1898; see his figs. 38 and 39 and especially figs.

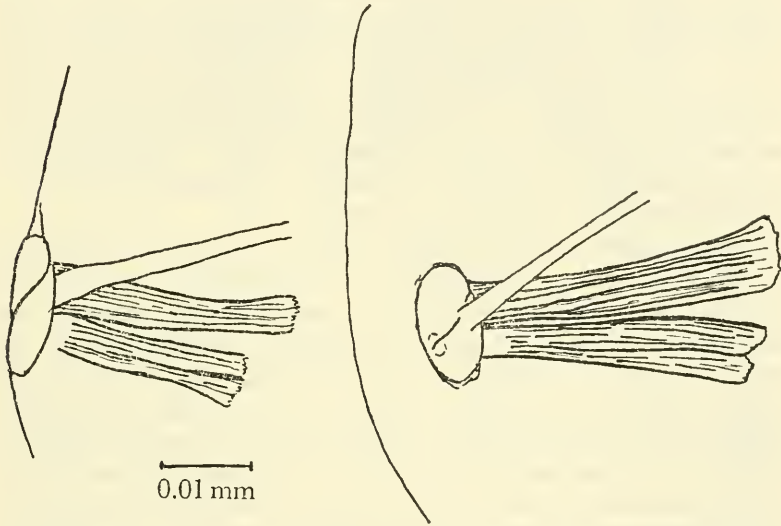


FIG. 1.—*Acercantomon doderoi* Silv. Pseudoculus with nerve and muscles seen from inside the cranium; the same pseudoculus from different angle.

77-83), that of *Protjapyx maior* Grassi by Silvestri (1933), who also gave a description of the mouth parts in what he calls the prelarva and the "larva primae aetatis" (see also Silvestri, 1948, pp. 284-286). The postlarval development of *Campodea*, especially *C. rhopalota* Denis, was studied by Orelli (1956), who, however, does not give figures of the mouth parts, but I have been allowed to see some of his slides, for which I am very grateful.

Uzel describes how just before the invagination of the embryo into the yolk (the blastokinesis) a fold appears lateral to the mouth parts, extending from the second maxillae to the intercalary segment. This fold, which later was given the name *plica oralis*, in its growth will enclose the mandibles and first maxillae in a cavity ventrally closed

by the second maxillae which unite to form the labium. This cavity is formed when the embryo is ready to hatch. Uzel also describes how both the first and second maxillae undergo rotation, as follows: Simultaneously with the first appearance of the fold the anlage of the first maxilla divides into an outer and an inner part; immediately afterward, when the anlage of the hypopharynx is appearing, the outer one turns forward in an oblique position to the inner one, then divides into two, the lobus externus and the palpus, and then returns to its original position. The second maxilla undergoes the same division and rotation, but before the first maxilla has returned, the second maxilla is back again and even continues this rotation so that the lobus externus finally lies anteriorly to the palpus. (Denis, 1949, p. 181, will not admit this interpretation, according to which the palpi-form lobus of *Campodea* is not the palpus as in *Japyx*, but the lobus externus; Bitsch, 1952, however showed it to be an indigenous structure of *Campodea*. Bitsch also doubts the existence of the rotation seen by Uzel, but I do not quite see why.)

It is important to notice that the figures in Uzel show the head of the embryo seen from in front, that is to say that one cannot see the length of the mouth parts. Silvestri in 1933 describes minutely the development of the mouth parts in *Protjapyx maior*, but he too, in most of his figures, depicts the head as seen from in front. The description of the plicae orales is exactly as in *Campodea*, and from his figures it appears that a similar, though less pronounced, rotation of the first and second maxilla takes place. In his figures II₅ and III₁₋₂, however, the head is seen in a more ventral or lateral view, and from these it appears that before the rotation of the second maxilla the mandible does not proceed farther backward than the first maxilla, as is the case in the adult animal. Unfortunately, figure III₃, of the head of the prelarva (the last stage in the egg), does not show the mandible.

Protjapyx (Silvestri, 1933 and 1948) emerges as a first-stage larva, "larva primae aetatis," which, however, is nearly immobile and yet lasts 5 to 6 days, when after a moult it develops into the second larval stage, also nearly immobile and morphologically different from the following stages. *Campodea* (Orelli, 1956) emerges as a prolarva, which lasts only a few minutes and then develops into a larva neonata, both morphologically different from the following stages. The prolarva and the larva neonata in *Campodea* seem to correspond to the larvae primae and secundae aetatis in *Protjapyx*. The first larval (prolarval) mouth parts of *Protjapyx* are figured and described by Silvestri (1933, p. 335 and fig. III₆₋₉); the mandibles have only two

teeth, the lobus internus of the first maxillae have no setae, and the palpi are unsegmented. Unfortunately, the mouth parts are not drawn in the head capsule.

The prolarval mouth parts of *Campodea* are drawn in figure 2 in ventral view after a slide made by Orelli. It is seen that they are very much like those of the adult, the mandibles possessing all teeth and

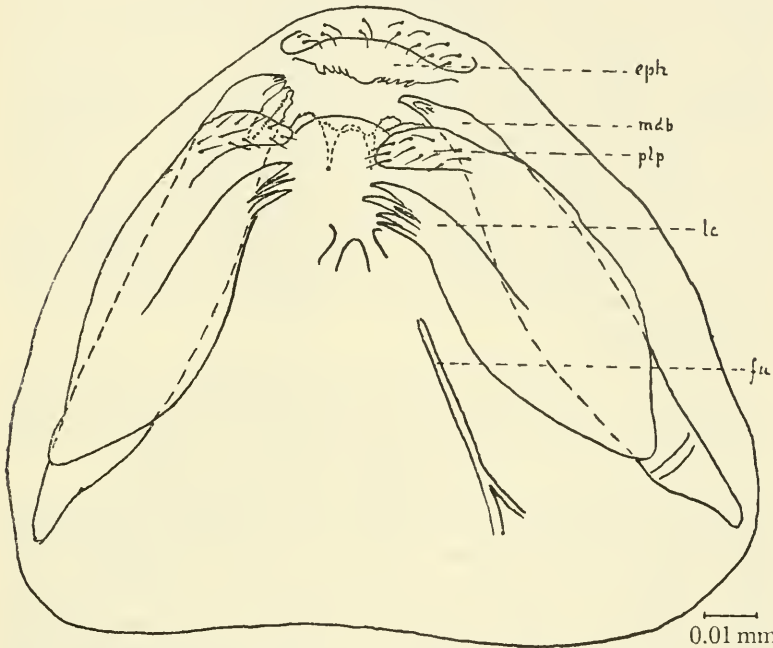


FIG. 2.—*Campodea rhopalota* Denis. Prolarva. Head, ventral, antennae omitted.

also the prostheca characteristic of *Campodea*, and the lobus internus of the maxilla having all setae. The lobus externus could not be seen. The important point is, however, that though the hypopharynx has its final shape, the sternal sclerotization, the fulcrum, is only indicated. It is also seen that the mandible proceeds farther backward than the maxillae.

The embryology of *Anurida* (Collembola) is best described by Folsom (1900), who, with regard to the mouth parts, says that a fold appears on each side of the head in the region of the mandibles and proceeds forward and backward to the fundaments of the labrum and the labium, involving the labial and clypeal folds "in such a way that all three folds become one and enclose a single common cavity." His

beautiful figures 5 and following show the development of this plica oralis, but besides views of the head from in front he gives also side views and purely ventral views, and from these it is seen that as long as the second maxillae are free the mandibles and first maxillae occupy a normal position to the rest of the head (stage 5, figs. 20, 21), but when the labium is coalesced with the oral folds the other mouth parts become long and as if retracted backward into the head (stage 7, figs. 24, 25, 29, 30). A rotation of the first maxillae as described by Uzel in *Campodea* is seen by comparing figures 11 (stage 3) and 12 (stage 4) with figures 21 (stage 5) and 29 (stage 7). A corresponding rotation of the second maxillae cannot be seen, as lobi externi as well as the palpi are lacking. Folsom states expressly as his opinion (p. 139) that "the entire gular region is labial in origin." He also notes that the lingua and superlinguae (glossa and paraglossae) develop independently of the fulcrum (his basal stalks), which latter form "in a groove which is but a longitudinal evagination of the maxillary pocket" (p. 111). In stage 7 (fig. 29) this stalk is said to be fully developed.

The postembryonal development of Collembola has been investigated by several workers, most recently by Lindenmann (1950), but a description of the mouth parts and the head of the very first stages is nowhere given and I have not seen any specimens myself.

The embryology of Protura is unknown. As to the postembryonal development, it has been known since Berlese that they have anamorphosis, and the present author (Tuxen, 1949) has definitely determined the kind of anamorphosis. I distinguished a prelarval stage with 9 abdominal segments and very different from the following stages, and after this stages with 9, 10, 12, and 12 segments before the adult stage. There is no doubt in my mind that my prelarva corresponds to the prolarva in the development of *Campodea* and *Japyx* (see above), and I willingly change the name from prelarva into prolarva. But I am strongly opposed to the names proposed by Paclt (1956b, p. 59), who substitutes the word nymph for the word larva and further introduces the words protonymphs, deutonymphs, and tritonymphs, which have a definite meaning in arachnids not at all comparable with the present case. Also the change of larva into nymph seems to me superfluous, the rigid distinction between the names of juvenile stages with or without metamorphosis being unhappy as it suggests a distinction more fundamental than it really is (see also Imms, 1957, p. 224), and furthermore the word larva is always used in reference to apterygotes.

The prolarva of Protura is different from later stages in many

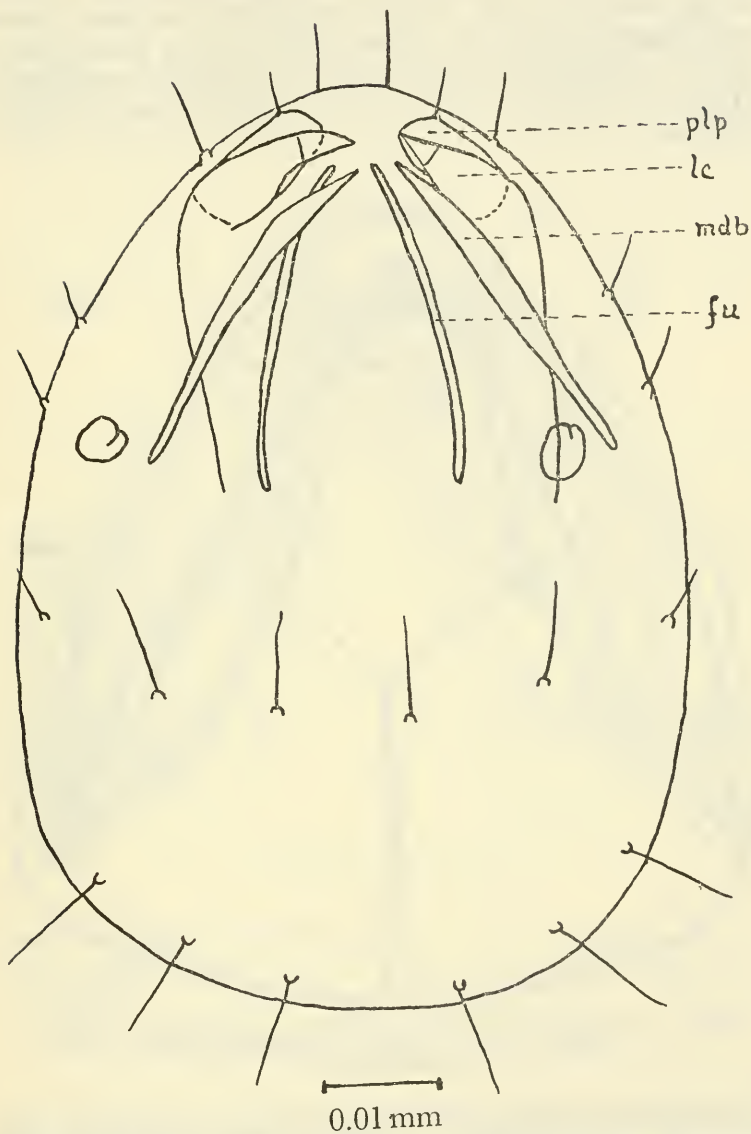


FIG. 3.—*Acerentulus danicus* Condé. Prolarva. Head, dorsal.
(After Tuxen, 1949.)

respects; here we are interested in the mouth parts (fig. 3) which are not finally developed: the maxillary palpus unsegmented, lacinia longitudinally undivided, labial palp without sensory papilla, and the fulcrum only indicated and their rods not coalesced in the middle line (Tuxen, 1949, pp. 33-34). The accordance with prolarva of Diplura is obvious.

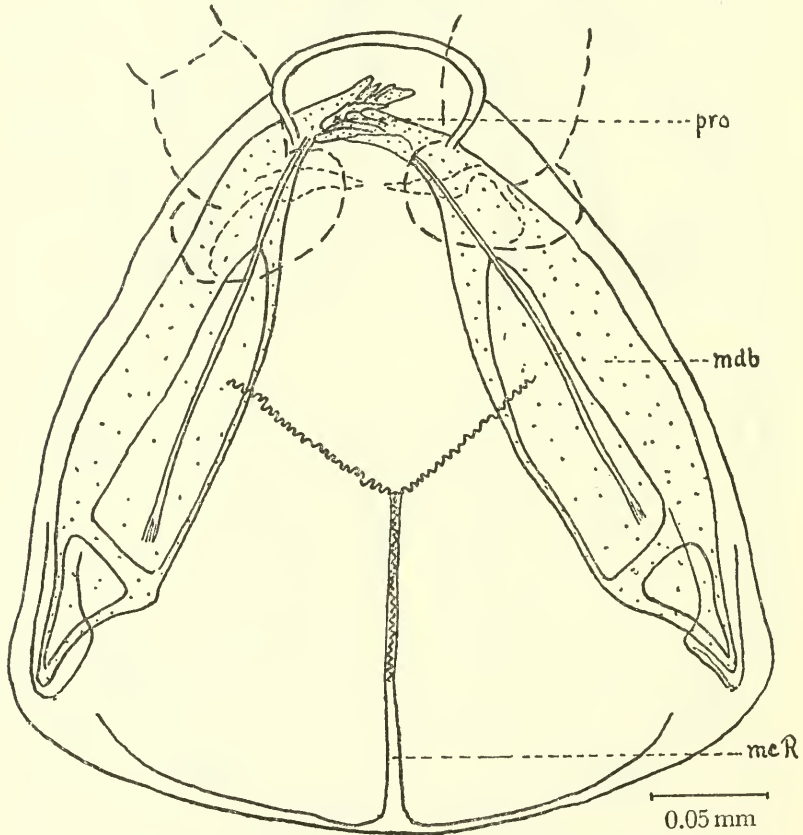


FIG. 4.—*Campodca plusiochaeta* Silv. Head with mandibles, dorsal. Mandible dotted.

Though the morphology of the mouth parts of Diplura has been described several times, I have made the figures 4-7 to form for myself an impression of the conditions. Figures 4 and 5 show the head from above, the mandibles and what is below the mandibles, figure 6 the mouth parts ventral, the labium removed, and figure 7 the head in side view—all in the same magnification. I had hoped on the basis

of these drawings to be able to give a series of cross sections of the head showing the shape of the atrium and the gnathal pouches, but this proved to be unsatisfactory without true microscopical sections. Nassonow (1887) has, however, given very convincing cross sections of the head of *Campodea "staphylinus"* anterior to the antennae (figs. 25 and 38), at the middle of the head (fig. 28) and at its hind

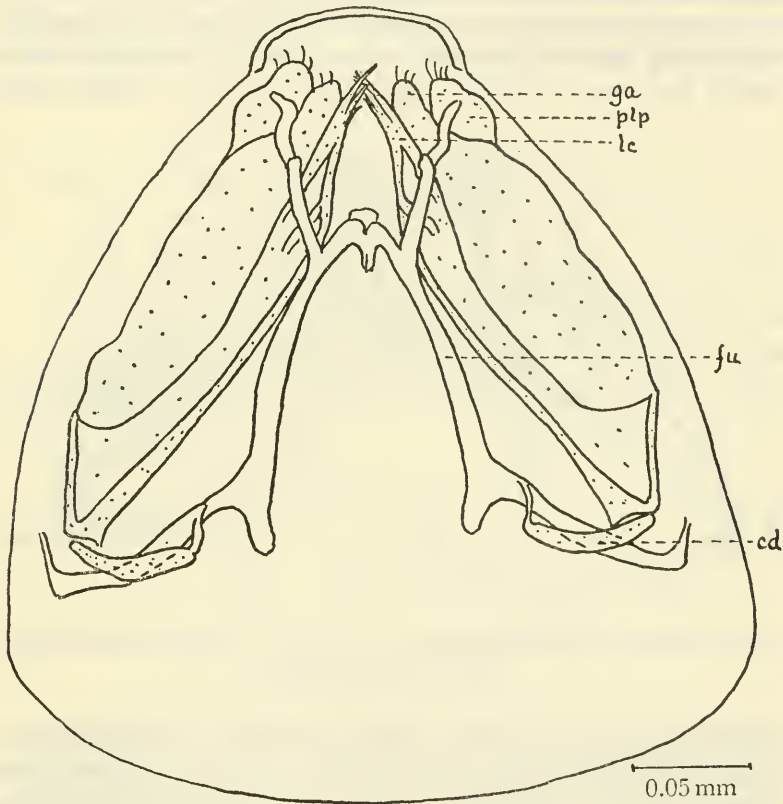


FIG. 5.—*Campodea plusiochaeta* Silv. Head with maxillae and fulcrum, dorsal, mandibles omitted. Maxillae dotted.

part (fig. 29), as well as before and behind the "appendages" of the labium (figs. 40 and 39). Snodgrass (1951, fig. 30 D) gives a cross section of the head of *Heterojapyx gallardi* Till.

The main points are the following: The mandibles and the maxillae are hollow at the inner and upper sides, especially distinct for the mandibles. The cavity contains the muscles as shown in a later chapter. At the original sternal part of the head is found a system of rods,

the fulcrum, which supports directly the maxillae and the superlinguae. The shape of this fulcrum will be discussed later. The mandibles extend farther back than the maxillae, in fact nearly reaching the hind border of the head (fig. 7); this shows that actually a reciprocal movement of the mandibles and the maxillae must have taken place, probably in connection with the rotation of the first and second maxillae during embryological development.

The pouch is distinctly seen behind the mandibles and the maxillae, surrounding both; it proceeds forward, but is interrupted in the middle line, where the sternal parts of the head are coalesced with

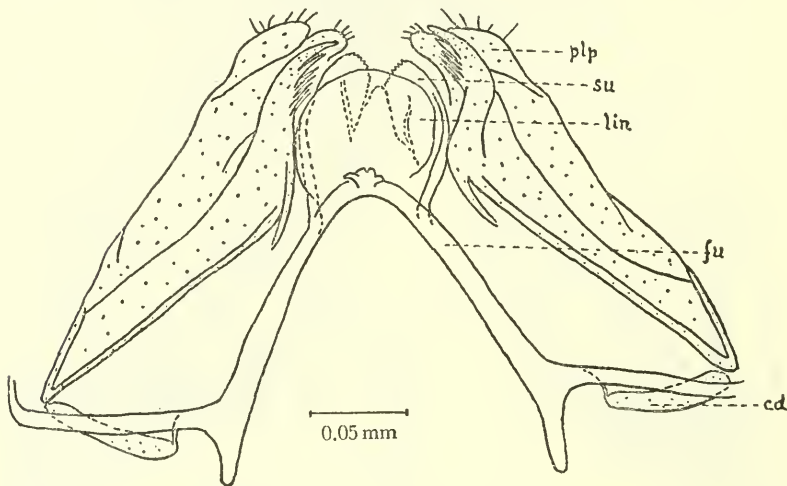


FIG. 6.—*Campodea plusiochaeta* Silv. Fulcrum, hypopharynx, and maxillae, ventral. Maxillae dotted.

the labium (see, for instance, Nasonow, fig. 28). The hypopharynx (lingua and superlinguae) is situated below the maxillae. The pouches extend very near to the side wall of the head (the plicae orales being very narrow) in their entire course and are open to the lateral exterior at the height of the maxillary palpi.

As an example of the morphology of the mouth parts of Collembola I shall give figures of *Onychiurus armatus* Tullb. (figs. 8-11) drawn from the same sides as figures 4-7. They have been drawn previously several times, most beautifully by Börner (1908); cross sections are found in Nasonow (1887, fig. 56 anterior to the antennae and fig. 57 in the middle of the head) and in Denis (1928), who also describes other species of collemboles. Beautiful cross sections are

given by Hoffmann in his two papers on *Tomocerus plumbeus* L. (1905 and 1908).

The important points to be noted are the following: The mandibles and the maxillae are hollow at the inner and upper sides just as in *Campodea*; a closer comparison of the single mouth parts will be given in a later section. The mandibles do not extend so far back as in *Campodea*, the relative position of these mouth parts being "normal"; on the other hand they extend more dorsally, very near to the roof of the head. A fulcrum is found similar to that of *Campodea*.

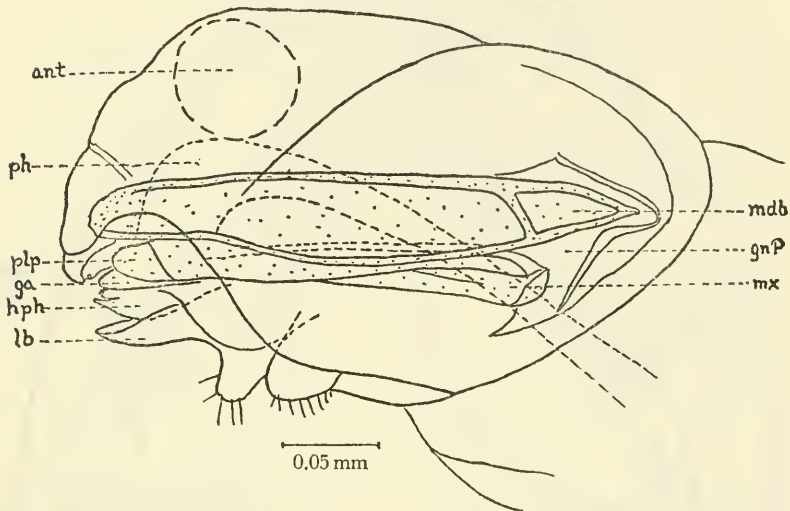


FIG. 7.—*Campodea plusiochacta* Silv. Head in side view. Mandible and maxilla dotted.

The pouch is broadest posteriorly surrounding both pairs of mouth parts (see figs. 8 and 11) and narrowing anteriorly, the anterior split of the atrium (the "mouth") being much narrower than in *Campodea*. The sternal wall of the head is coalesced in the middle line with the labium in the hind part of the head (Denis, 1928, figs. 37-38; unfortunately it is often difficult to make clear where the sections are laid), but free more anteriorly where the hypopharynx is found (Denis, fig. 31). The maxillae intrude between the lingua and superlinguae of hypopharynx (Denis, loc. cit.; my figs. 10 and 11).

The labium is the well-known triangular piece far anterior on the under side of the head. The part behind this piece (or rather pair of pieces) is commonly regarded as the submentum, but a limit between submentum and plicae orales is not found and Hoffmann (1911) men-

tions that the proximal part of the labium is dissolved after having been overgrown by the plicae, which leave between them the ventral groove. A thorough study of the labium and its musculature in *Collembola* in the same fine way as the study by Bitsch on *Diplura* is much needed.

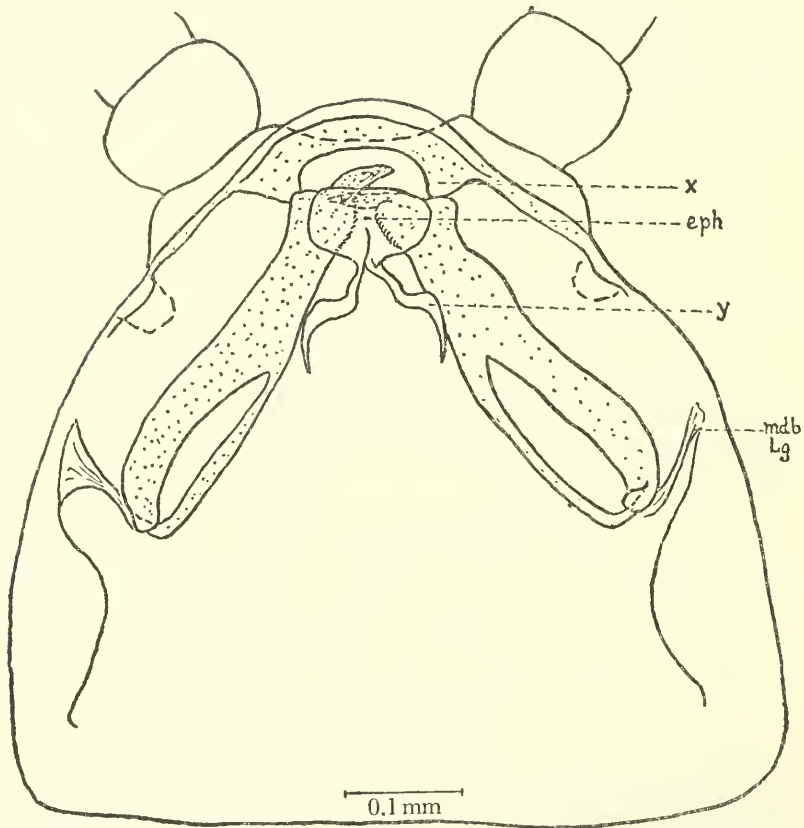


FIG. 8.—*Onychiurus armatus* Tullb. Head with mandibles, dorsal. (*x* and *y*, see text.)

Figures 12-14 show the mouth parts of *Acerentomon doderoi* Silv. as an example of the conditions in Protura. Berlese (1909) has given excellent descriptions and in his figures 128-135 (Tav. XIII) most enlightening cross sections of the head. In 1952 I myself published other drawings dealing especially with the so-called tentorium, the fulcrum.

The main points are the following: The maxillae are hollow on the inner side, whereas the mandibles are not hollow. A fulcrum, the

so-called tentorium, is present, not V-shaped, but Y-shaped, the lateral branches being coalesced to a large extent. From this fulcrum branches are given off to the clypeus and two short dorsal arms at the middle. A hypopharynx is absent. The mandibles extend backward to a little behind the roots of the maxillae, but as they are very movable within the head their exact position is not easily defined.

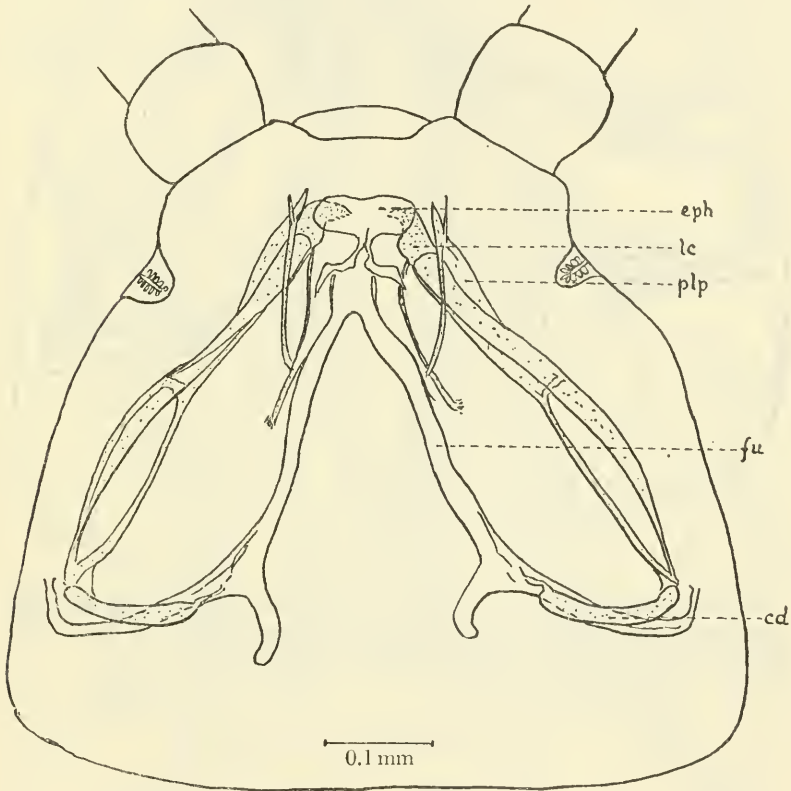


FIG. 9.—*Onychinrus armatus* Tullb. Head with maxillae and fulcrum, dorsal, mandible omitted. Maxillae dotted.

The shape of the gnathal pouches is not easily seen, but from figure 14 it appears that the maxillary pouch is very broad anteriorly where it contains the palpus. At this place it is continuous with the mandibular pouch, but in the hind part of the head no such connection seems to be present. Cross sections may decide.

The labium is a small triangular piece as in *Collembola* with distinct palpi, but also with structures parallel to what Hoffmann (1908,

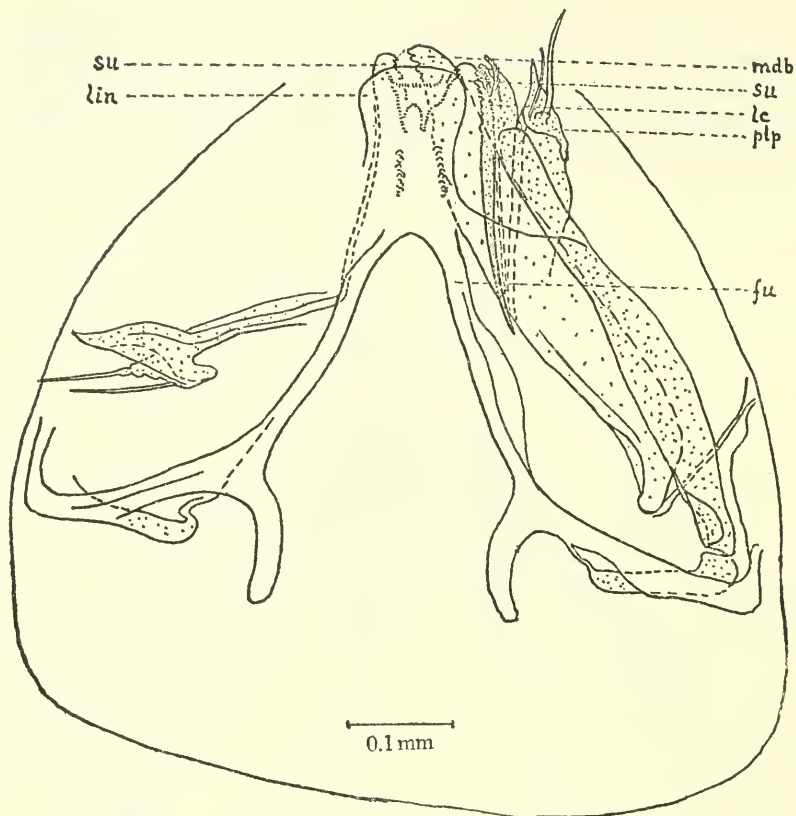


FIG. 10.—*Onychiurus armatus* Tullb. Fulcrum, hypopharynx, and left mandible and maxilla, ventral. Mandible openly dotted, maxillae closely dotted. The right galea and palpus are also seen in a detached position.

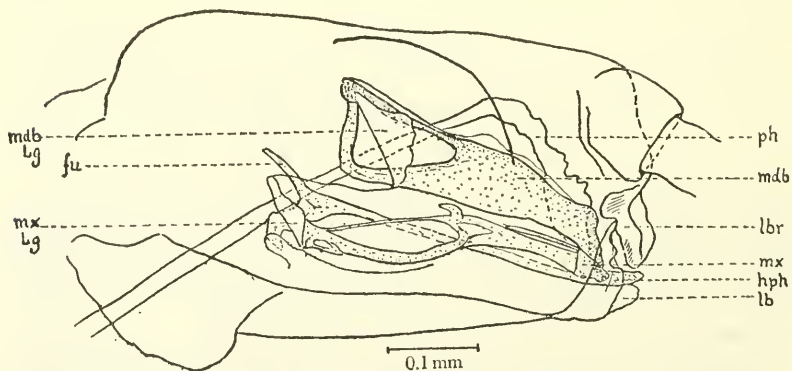


FIG. 11.—*Onychiurus armatus* Tullb. Head in side view. Mandible, maxilla, and fulcrum + hypopharynx dotted.

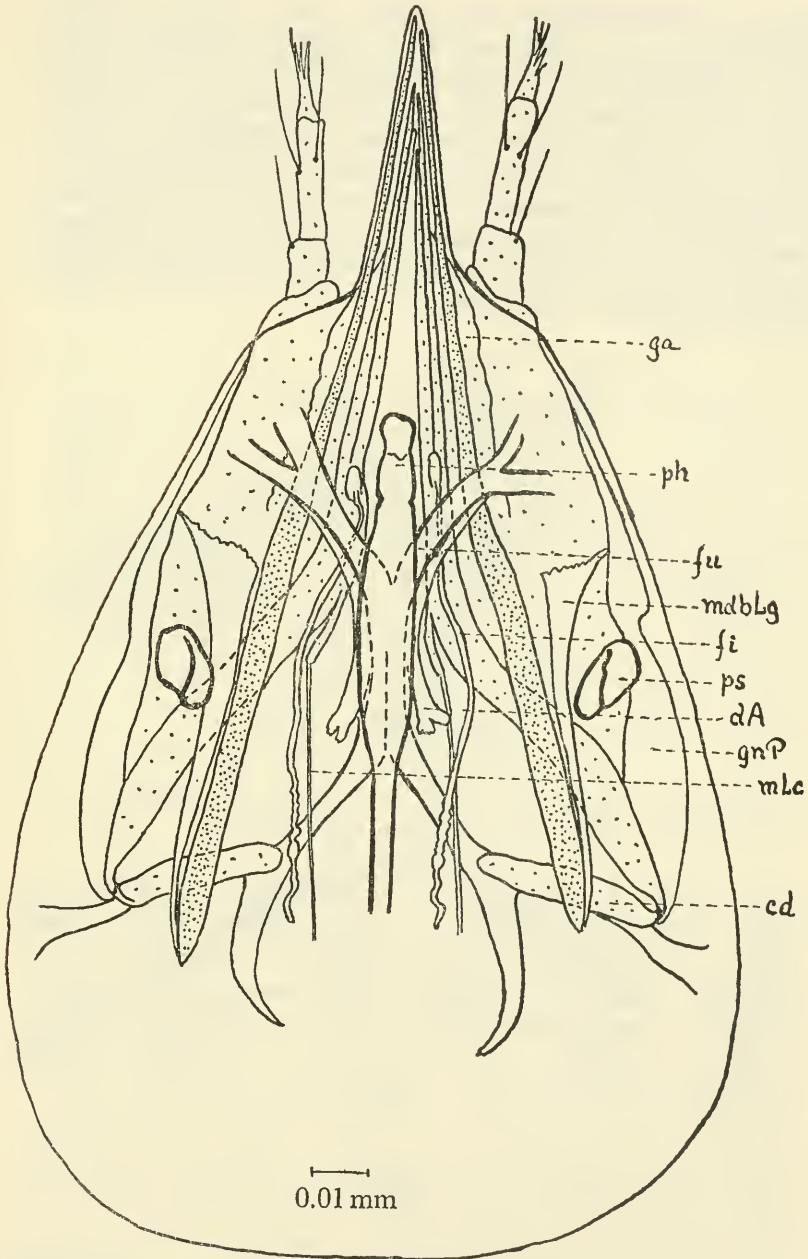


FIG. 12.—*Acerentomon doderoi* Silv. Head, dorsal. Mandibles closely dotted, maxillae openly dotted. The drawing of the distal part of the mouth parts somewhat schematical.

p. 650) calls "Klauenteil" and "hyaline Platte." This has not been drawn by anyone, but I have seen it in different species and shall later present drawings. Behind this piece (or rather pair of pieces) the sides of the head approach each other, leaving between them a very narrow groove in which a structure called the gula is said to be found (Prell, 1913); I have not been able to find this (see fig. 13). The groove may be comparable to the ventral groove of Collembola, though it does not continue on the thorax and its function is unknown. Also the labium of Protura needs a thorough study, which was not feasible at the time of this writing.

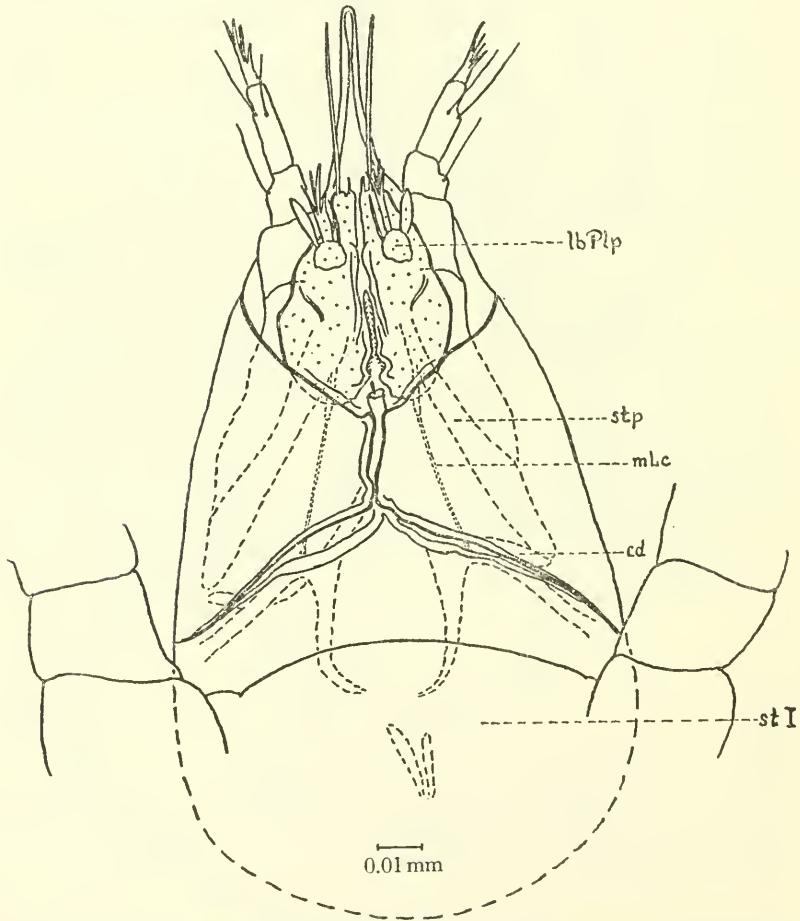


FIG. 13.—*Acerentomon doderoi* Silv. Head, ventral. Labium dotted. Proximal part of fulcrum and maxillae shown by dash lines. Prosternum artificially withdrawn from the head.

From this it would seem evident that entognathy in the entognathous apterygotes is a rather complex business. It results first and foremost from the building on either side of the head between labrum and labium of a plica oralis which coalesces with the labium, forming one or two pouches on each side enclosing the mandibles and maxillae. At the inner edges of these pouches some stiffenings arise, forming the fulcrum, which also carries the hypopharynx if such a structure is present. But besides this the following happens: 1, The sternal part of the head coalesces in the middle line with the labium. 2, The mandibles (in Diplura and Collembola) and the maxillae (in all three

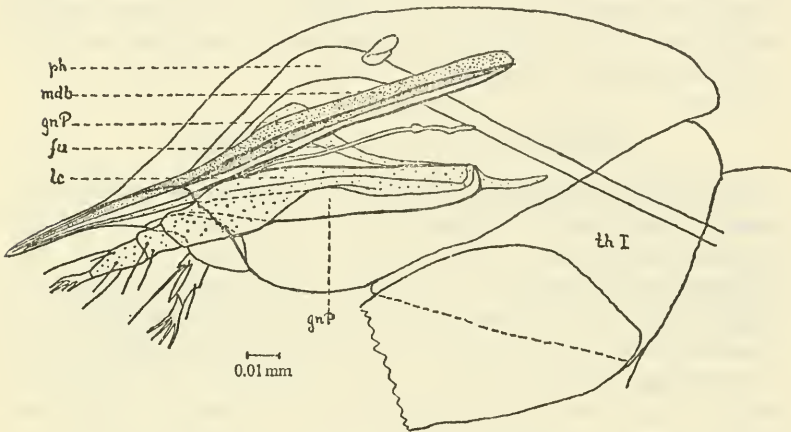


FIG. 14.—*Acerentomon doderoi* Silv. Head in side view. Mandible closely dotted, maxilla and fulcrum openly dotted.

groups) become hollow at the side, turning against the interior of the head, and some of their muscles take their origin in these cavities. 3, The head, which is originally hypognathous, becomes more or less prognathous, the mandibles and maxillae turning from a vertical to a horizontal direction and simultaneously changing more or less their relative positions, the mandibles extending in the Diplura and Protura farther back than the maxillae, reaching even the hindmost part of the head. Whether this change in relative position has any connection with a rotation noticed during embryogeny is not known. 4, The plicae orales, approaching the under side of the head, push the labium, or at least its anterior part, before it to the apex of the head, meeting in the middle line or leaving a smaller or broader remnant of submentum between them.

The entognathy therefore seems to me to arise not only by way of

the plicae orales, but also by "ingrowth" of the mandibles and maxillae into the head. It is true that Philiptschenko (1912, p. 578) expressly states, in accordance with Folsom, that "die Mundorgane werden durchaus nicht in das Innere des Kopfes verlagert," but I think that the final position of mandibles and maxillae in Diplura and Protura proves this ingrowth, also indicated in Collembola by the nearness of the mandibles to the roof of the head; and furthermore the position of cardo dorsal to fulcrum—if it is in fact the cardo, as I shall discuss later—in my opinion supports this view. In this way, out of the hypognathous head is shaped a prognathous one in a manner entirely different from that by which prognathous heads are formed in the other insect groups. The formation of the fulcrum and the "dissolution," so to speak, of the mandibles and maxillae, are direct consequences of these changes.

3. THE HYPOPHARYNX AND FULCRUM

The hypopharynx and the fulcrum are two independent structures, though it might seem as though the fulcrum is only a skeleton supporting the hypopharynx. This last-named structure is present only in Diplura and Collembola; in Protura I have found no trace of it, though Prell (1913) depicts "ein kielförmiges Mittelstück" corresponding to the lingua and even "eine Reihe feiner Chitinstäbchen" corresponding to the superlinguae. The hypopharynx in the other two groups is very much alike, consisting of a membranous lingua ventrally and two superlinguae more or less toothed on the inner edge. The superlinguae are supported by branches from the fulcrum.

The fulcrum itself consists of two retrograde diverging stalks proximally biramously divided into a short median branch and a longer lateral one reaching the lateral walls of the head. To this lateral branch a rod is attached by a ligament. This rod is commonly regarded as the cardo of the maxilla, but it should be noted that it is placed dorsally to the lateral branch of the fulcrum, so if it really is the cardo, this would indicate that the maxilla during development must have grown backward "into the head." It is very much alike in all groups and gives attachment in its distal part to muscles, which fact might support the conception of it as a cardo.

The shape of the fulcrum is very much alike in Diplura and Collembola, whereas the two branches in Protura coalesce in the middle line. Branches are given off anteriorly, supporting the superlinguae in Diplura and Collembola (figs. 6 and 10), and in Protura to the sides of the "clypeus"; in Diplura the clypeus has a supporting sclerotiza-

tion of its own (fig. 4). In Protura also two "dorsal arms" are given off from the coalesced middle part; from their position they seem to support the two large basal muscles of the maxillae, though I have not been able to follow this in detail. They were hitherto found only in *Acerentomon*.

As already pointed out, the fulcrum in Diplura and Protura develops later than the mouth parts and, in Diplura, the hypopharynx; in Collembola, however, it would seem from Folsom (1900, fig. 25) that they have already attained their connection with the hypopharynx in stage 7, i.e., before hatching.

A true tentorium is not found in any of the three groups. In Collembola Denis (1928) described a very elaborate structure which he calls tentorium, but which, being mesodermal, cannot be compared with the tentorium of Thysanura and Pterygota. Snodgrass (1951, p. 87) points out that "it has the appearance of being a tissue comparable to the endosternum of Arachnida." It has been termed "architentorium" by Hansen (1930), and Paclt (1956b) follows him, but this term also is unhappy, the structure being no forerunner of a tentorium. I propose to call it endosternum. A similar endosternum is present in *Campodea* (see Nassonow, 1887), though I have not been able to trace it in my slides. The ending of some muscles, however, shows its presence (fig. 15). And also in Protura I suppose an endosternum to be present, though I have never seen it.

4. THE MANDIBLES

The mandibles in Diplura are hollow at the inner and upper side and for nearly four-fifths of their length apart from the teeth. One-fifth of the distance from the proximal end a sclerotized rod bridges this cavity. In *Campodea* a separate prosthca is found, already seen by Meinert (1865), to whose beautiful drawings the student should still be referred; a long ligamentous cord connects this prosthca with two muscles at the hind part of the head (fig. 15, *b*). A prosthca is absent in *Japyx*. The proximal end of the mandible lies free in the gnathal pouch, no supporting rods being found.

Among the muscles the following may be pointed out (fig. 15): The three muscles *c* and *d* run from the roof of the head to the dorsal side of the mandibles retracting them. Two muscles, *f*, from the dorsal side of the mandible to the endosternum are placed dorsal to the ligament of the prosthca. An oblique muscle, *g*, runs from the underside of the bridging rod to the endosternum, below the said ligament. Proximal to *f* the two muscles *e* and *i* run from the dorsal

side of the mandible to the roof of the head and its hind wall, respectively. And finally the muscles *h* are seen, a lot of muscles radiating from the entire inside of the cavity of the mandible and uniting

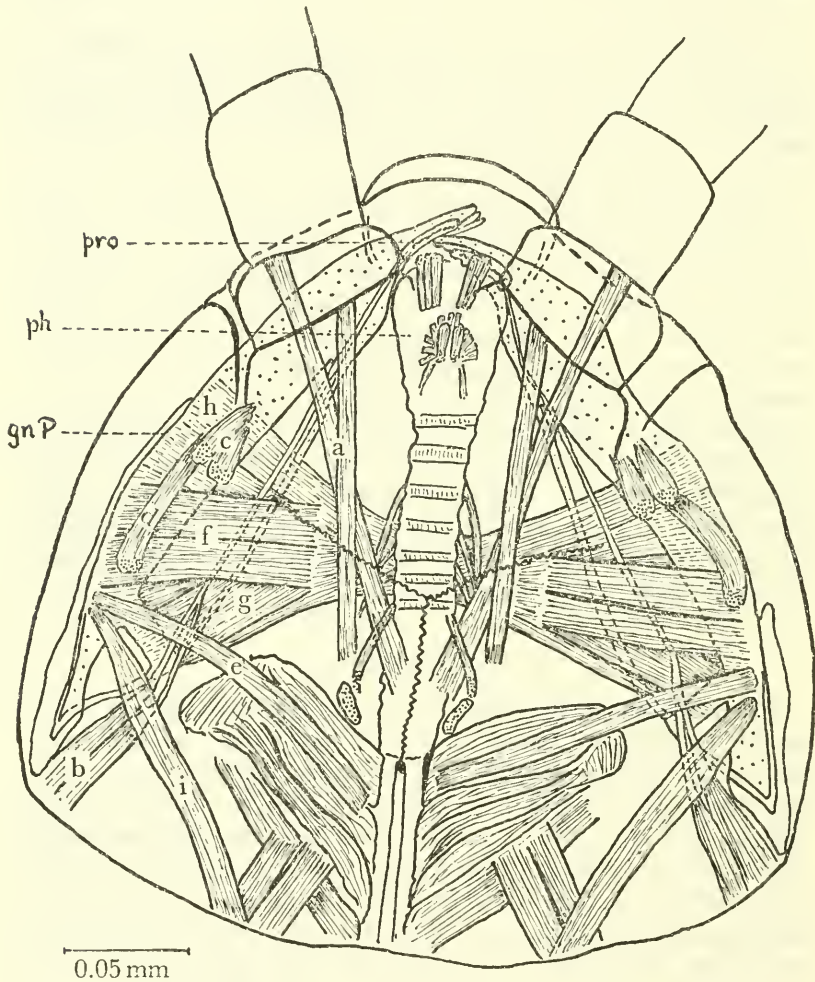


FIG. 15.—*Campodea plusiochaeta* Silv. Head, dorsal, with antennal (*a*) and mandibular muscles (*b-i*); see text.

below the oesophagus with the corresponding ones from the mandible of the other side; a broad ligamentous band connects them. The other muscles in figure 15 are antennal muscles (*a*) or head muscles without connection with the mouth parts; they have been drawn be-

cause they are a very characteristic feature of the slides and seem to a large extent to be connected with what Snodgrass (1951) called the midcranial ridge and which should not be confused with the epicranial suture (both are indicated in figures 4 and 15). On the pharynx are seen some muscles from the roof of the head.

The mandibles of Collembola are also hollow at the inner and upper side, but only to less than half their length apart from the teeth. No rod bridges the cavity. A prosthema is not present nor any muscle corresponding to *b* in Diplura. From the wall of the head just below the antennae a process (fig. 8, *x*) meets a hump on the back of the mandibles, thus yielding support to their movements. Also some branches, *y*, from the epipharynx seem to support them at their interior side. From the proximal end, which carries a condyle, a fanlike ligament is seen running to the wall of the head (fig. 11) and forming part of the limitation of the gnathal pouch; this ligament in certain views may take the shape of a rod, but I do not think it is a real rod (as drawn by Snodgrass, 1951, p. 85, fig. 31 G) and so I am not convinced of its homologization with the rod of Chilopoda.

A comparison with the muscles in Diplura has been tried (fig. 16): The two muscles *c* are strongly developed, whereas *d* is not found. Two muscles, *e*, are present, crossing the middle line of the head and attached to its dorsal wall on the other side. The straight muscles *f* to the endosternum were not found, but only the oblique one *g*. Also a muscle, probably corresponding to *i*, is present, though it does not run to the hind wall of the head, but only to its dorsal wall somewhat behind the attachment of *e*. And finally the muscles *h* which meet the corresponding ones from the opposite mandible below the oesophagus are not dispersed fanlike as in *Campodea*, certainly because of the much smaller cavity in *Onychiurus*. A comparison with Denis's figure (1928, p. 112) would run as follows: $c=I$, $e=A+B$, $g=IV+V$, $h=VI$, $i=VII$. In the figure, furthermore, some antennal muscles, some characteristic cranial muscles, and some pharyngeal muscles have been drawn.

Denis (1928, p. 115) emphasizes the crossing of the muscles here called *e*, found only in a few groups of insects. As an example he mentions *Campodea* as figured by Nasonow (1887, Taf. 1, fig. 4), but that figure is incorrect; as my figure 15 shows, there is no crossing in *Campodea*, which as a matter of fact would seem to be prevented by the midcranial ridge.

The endosternum seemed visible to some extent in one of my slides and has been outlined around the oesophagus.

The mandibles of Protura are not hollow. They are long spearlike structures with a slitlike opening near the apex. Prell (1913, fig. 4) describes a rod from the proximal apex to the wall of the head, but I have not found this; perhaps it is the fanlike ligament (fig. 12) taking this aspect in certain views. Prell also describes the basal part of

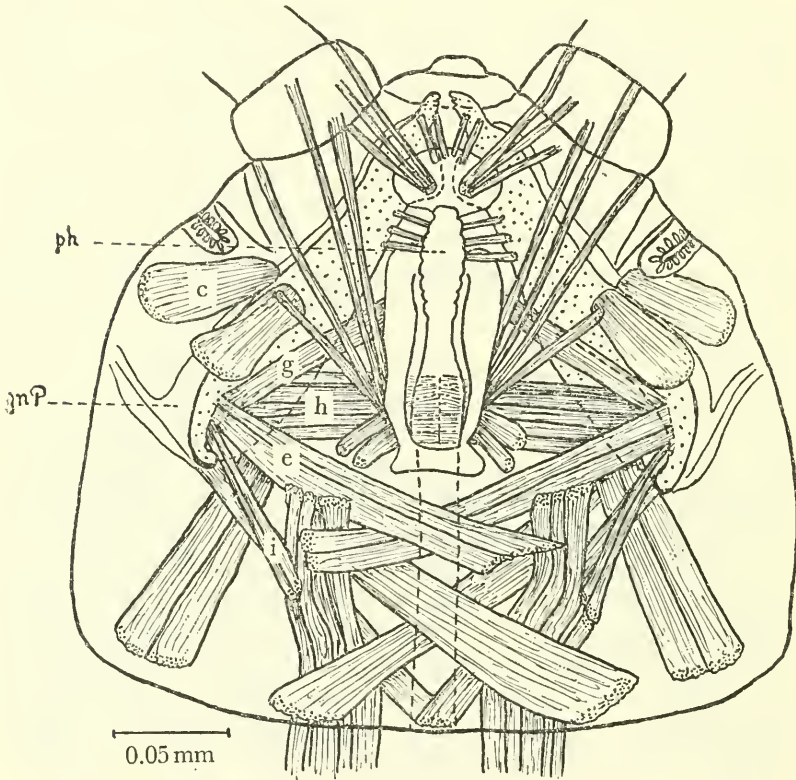


FIG. 16.—*Onychiurus armatus* Tullb. Head, dorsal, with antennal and mandibular muscles (*c-i*); see text.

the mandible of *Eosentomon* as hollow; the position of the muscles in *Acerentomon* does not seem to support this observation.

In figure 17 I have drawn the muscles of the mandibles as seen by me; my figure agrees rather closely with the figure by Berlese (1909, fig. 121). There are two sets of protractor muscles and two sets of retractors, a median and a lateral one, all originating near the proximal end of the mandible. The retractor muscles run to the lateral and dorsal wall of the head, respectively; of the protractors

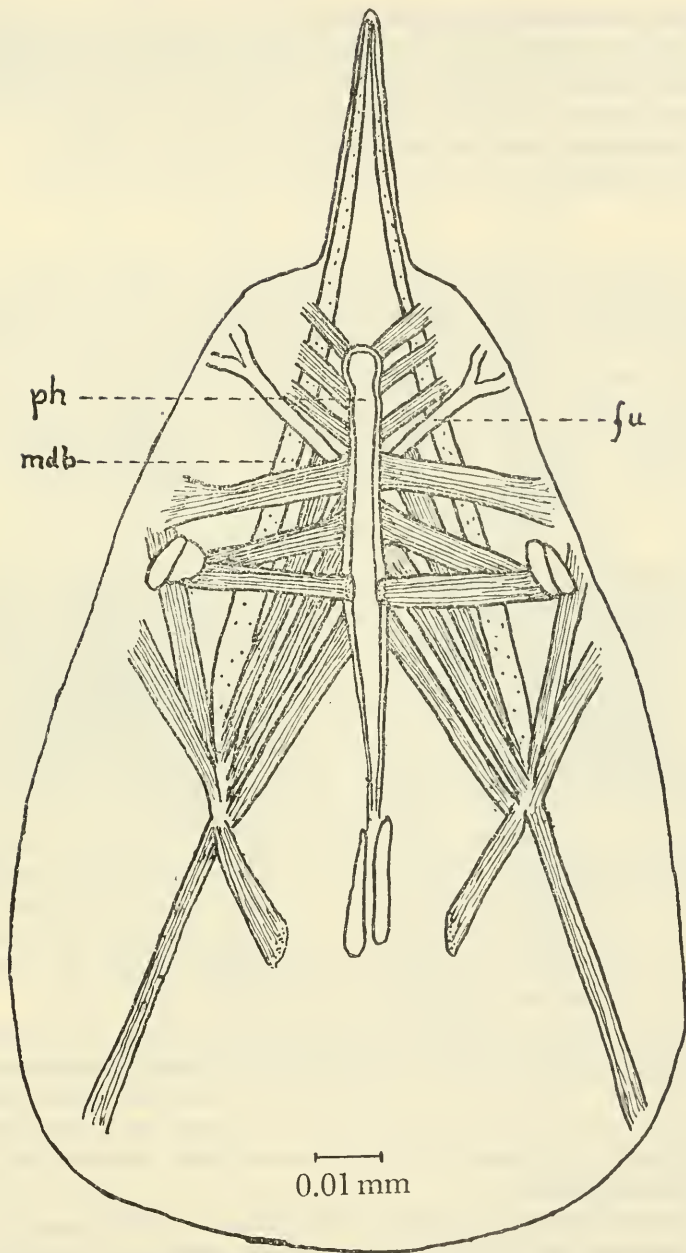


FIG. 17.—*Accerentomon doderi* Silv. Head, dorsal, with pharyngeal and mandibular muscles.

the lateral ones run to the lateral wall of the head, and the most distal of the three median ones runs to the branch of the fulcrum supporting the clypeus, whereas the other two median ones meet the corresponding ones from the opposite side beneath the oesophagus. They may correspond to the muscles *h* in the two preceding groups.

An endosternum has not been seen by me, but may be present.

From this it will be seen that the mandibles of the Diplura and Collembola are rather closely alike both in themselves and as regards their muscles, whereas the mandibles of Protura have a different musculature, are not hollow, and have no teeth. The mandibles of Protura are piercing organs necessitating especially strong protracting and retracting movements; and this, in connection with the probably secondary fact that they are not hollow, may account for the difference.

5. THE MAXILLAE

In Diplura the maxillae are hollow at their inner and upper sides. The basal rod is commonly called *cardo*; I have already mentioned that it is placed dorsally to the lateral proximal arm of the fulcrum. Since Meinert (1865), nearly all authors have regarded it as a *cardo*, the only exception known to me being Silvestri (1933); in figure IV₁₋₃ (p. 336) he designates a small proximal triangle of the stipes as *cardo* and does not give any name to the rod commonly called *cardo*. This small triangle is also seen by Hansen (1930, p. 129 and pl. VI, fig. 1b, *cp*), who calls it a "chitinized piece" and considers it a firmly chitinized small part of the membranous lateral wall of the head. It is not present in *Campodea* nor does it seem to me to be present in *Japyx*; at least in the cases I have seen myself—among which is also the slide made by Hansen and used for his figure—this piece is intimately connected with the *cardo* by weaker chitin.

A strong rod like a V with unequal arms forms the proximal end of the maxilla (figs. 5 and 6). The longer arm goes to the lacinia, the shorter arm continues in a weak part, the basal part of the palpus and galea, which are both well developed; in *Japyx* the palpus is even segmented. The palpus and galea are covered with hairs and are free of the mouth cavity.

This is the common explanation of the maxilla, and it seems to me quite natural; still Denis (1949) regards the whole piece between the fulcrum and the outer side of the palpus as the maxilla (called *cx*₁, *premier coxa*, by him), in which case the so-called *cardo* would be

only part of this coxa. This seems to me a quite artificial interpretation which, moreover, does not explain the rod from the lacinia to the proximal corner of the stipes (he quite ignores it in the drawing on p. 164).

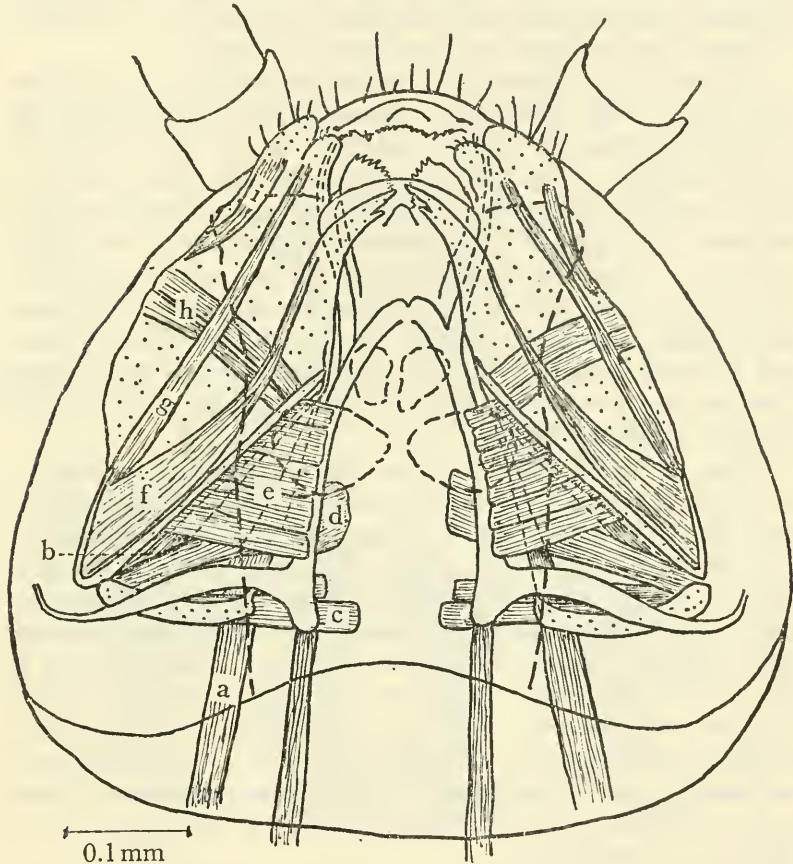


FIG. 18.—*Camphodea plusiochaeta* Silv. Head, ventral, with maxillary muscles (a-i); see text. Lacinia somewhat schematical. The outlines of the labium given in heavy dash lines.

The following maxillary muscles are to be noted from dorsally to ventrally (fig. 18): A dorsal muscle, *a*, from the ligament of the lacinia to the hind part of the head; another dorsal one, *b*, from the same ligament to the corner between the stipes and the cardo; two straight muscles, *c*, from this same point toward the middle, probably to the endosternum; an oblique one, *d*, from the same point to the

endosternum; and finally many parallel muscles, *e*, from the median side of the stipes to the fulcrum. Inside the maxilla a long muscle, *f*, is fanlike, originating from the lateral side of the stipes and running to the lateral side of the lacinia; another, narrower, one, *g*, runs to the galea; a broad one (or rather two), *h*, connects the median side of the stipes with the outside of the basis of the palpus; and a small one, *i*, connects this part with the distal part of the palpus.

The maxilla of Collembola is also hollow at the inner and upper side; in the middle a rod bridges this cavity. Its anterior end is the "Maxillenkopf" as it is called by Börner; its very fine structures in *Tetrodontophora* are drawn excellently by Börner (1908, Taf. VII, fig. 12) and are alike in *Onychiurus*. It seems to be homologous with the lacinia in Diplura. On the outer and anterior side of the stipes a structure is found (drawn separately in fig. 10), which corresponds to the palpus and galea. It is connected by a rod with the ligament of the superlinguae (?). The cardo is very much like that of Diplura and is placed dorsally to the lateral branch of the fulcrum. Denis gives an interpretation of the collembolan maxilla which parallels his views regarding Diplura.

Figure 19 shows some important muscles, viz, from dorsally to ventrally: Two muscles, *a*, running from the distal part of the stipes to the hind wall of the head; two muscles, *b*, from the basal part of the stipes and the distal part of the cardo to the middle of the head, where they meet the ones from the opposite side below the oesophagus; further, *c* and *d* attaching a ligament from the lacinia to the stipes and the cardo, respectively; an oblique muscle, *e*, from the stipes to the fulcrum; two oblique ones, *f*, from the cardo and the stipes to the fulcrum; and two straight ones, *g*, from the stipes to the fulcrum. A comparison with Denis's drawing of *Tomocerus* (1928, p. 163—and he himself says that conditions are identical in *Onychiurus*) would give the following identifications: $b=X$, $c=I$, $d=II$, $e=V$, $g=VI+VII$, $f=VIII+IX$.

A comparison with *Campodea* shows the following points: The muscle *a* in *Campodea*, running to the hind part of the head, is lacking in *Onychiurus*, but the other two lacinial muscles correspond (b and f in *Campodea*= d and c in *Onychiurus*). The oblique and straight muscles d and e in *Campodea* correspond to f and g in *Onychiurus*; and b in *Onychiurus*= c in *Campodea*.

The maxilla of Protura is hollow at the inner side; the upper side, in contrast to conditions in the other groups, is broader than the ventral side. There is a cardo similar to that of the other groups. The

hollow part is called the stipes; it continues in two long, pointed awls called lacinia 1 and 2, and a more bladelike part with wavy edge, called the galea. At the uniting (or diverging) point between the two lacinia (figs. 20 and 21) the so-called filamento di sostegno opens, a structure the morphological and physiological significance of which

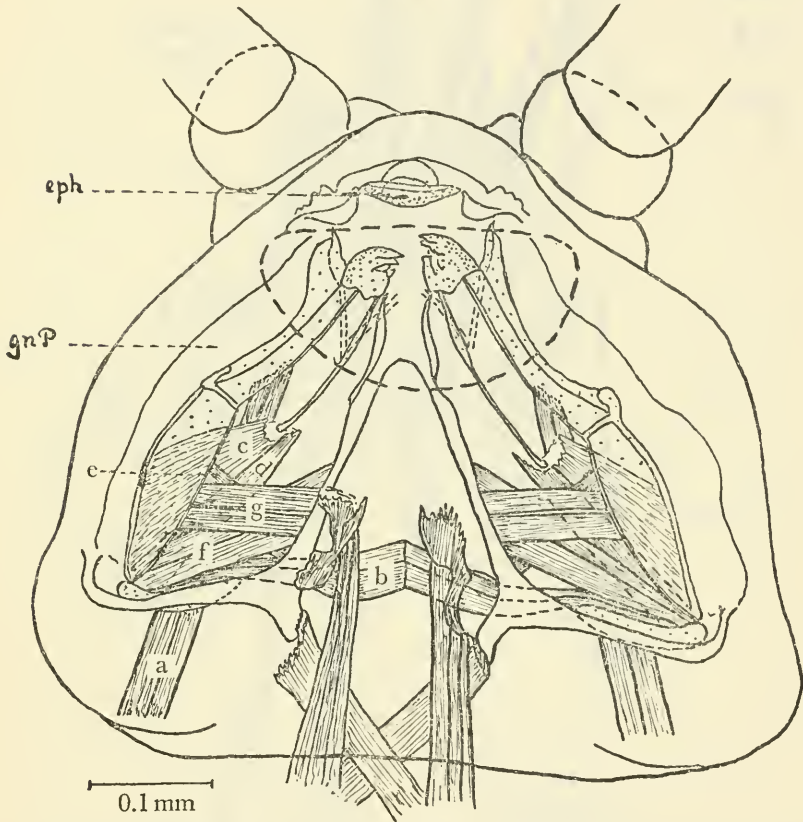


FIG. 19.—*Onychiurus armatus* Tullb. Head, ventral, with maxillary muscles (a-g); see text. The outlines of the labium given in heavy dash lines.

is unknown. An elliptic opening is found on lacinia 2 (fig. 21); this might indicate that filamento di sostegno is the duct of a gland, but Berlese (1909, p. 104) expressly states that it is solid. To the lateral side of the stipes a 3- or 4-segmented palp is attached.

Only very few muscles are present in connection with the maxilla (fig. 22), viz, three muscles, *a*, from the edge of the stipes to fulcrum, and two muscles, *b*, from the inside of the stipes to the fulcrum; very

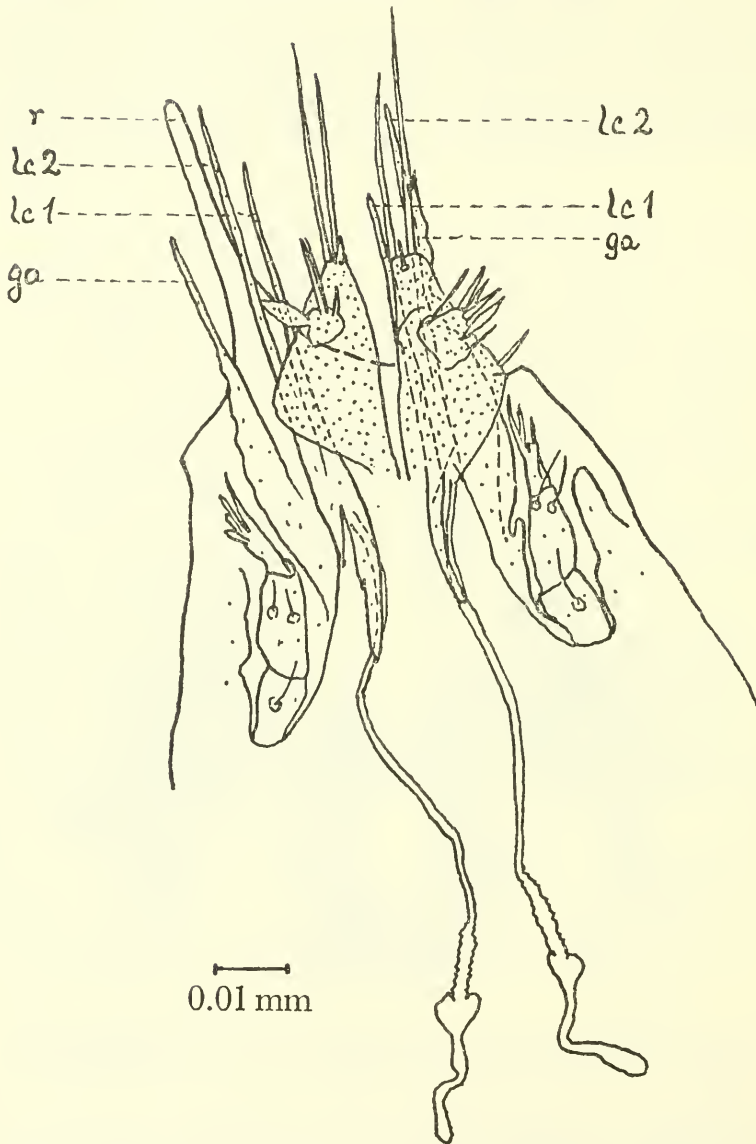


FIG. 20.—*Accerentomon doderoi* Silv. Fore part of head with mouth parts loosened from rostrum and palpi withdrawn. (After a slide in the Berlese collection in Firenze, No. 5.2.) Labium closely dotted, maxillae openly dotted.

probably the last-named muscles attach to the so-called dorsal arms of the fulcrum. Furthermore, a very thin muscle from the hind wall of the head is attached through a long ligament (*mLc*) to the median outgrowth of a sclerotized plate from lacinia 1, corresponding to the muscle *a* in *Campodea*, except that it is placed ventrally to the other

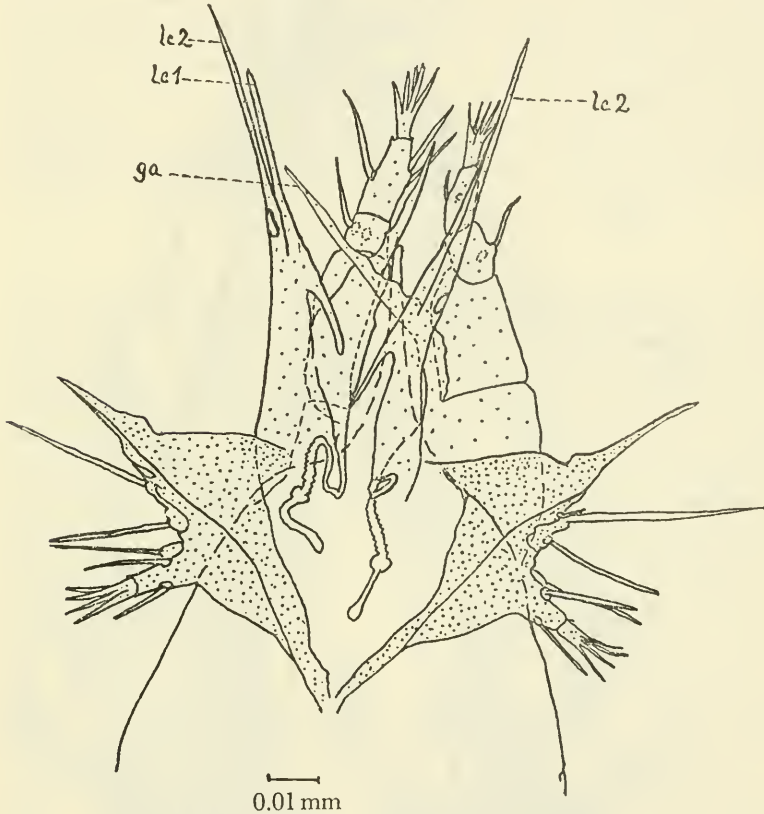


FIG. 21.—*Acerentomon doderoi* Silv. Fore part of head with the two halves of labium spread out and the maxillae as if spread out. (After a slide in the Berlese collection in Firenze, No. 3.8.) Labium closely dotted, maxillae openly dotted.

muscles in *Acerentomon*. And finally a palpal muscle, *c*, is found running from the proximal part of the stipes to the basal part of the first palpal joint (what Berlese calls the second joint). Berlese (Tav. V, fig. 36) has drawn this muscle to the very tip of the palpus, but I have not been able to follow it so far, nor is it very probable, because, as figure 20 shows, the outermost segments in retraction are unchanged.

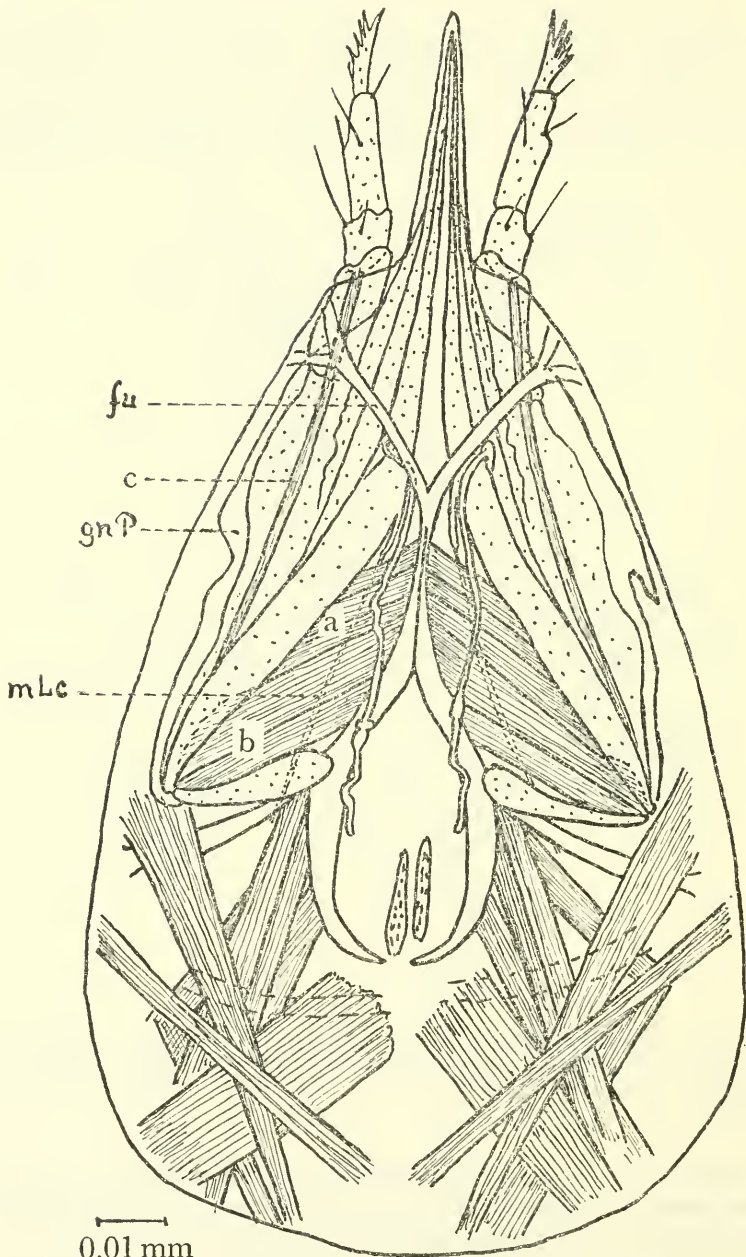


FIG. 22.—*Accrentomon doderoi* Silv. Head, dorsal, with maxillary muscles (a-c); see text. The mandibular muscles omitted.

From this it is seen that the general plan of the maxilla in the three groups is very much alike; especially the shape and position of the cardo are identical. The palpus is greatly reduced in most Collembola and without muscle, which, however, is present in Diplura and Protura. Also the galea is much reduced in Collembola. In all three groups the lacinia carries an arm or platelike process to which one or more muscles are attached, running to the stipes, to the hind wall of the head, or to both. And in all three groups powerful muscles connect the stipes and the distal part of the cardo, as it seems, to the fulcrum. In Diplura and Collembola some dorsal muscles from the stipes join the corresponding ones from the opposite side below the oesophagus; this is not the case in Protura, the maxillae of which are extensively modified into piercing organs.

6. CONCLUSIONS

It is my hope that this comparison between selected types of the three groups of entognathous apterygotes will have shown how great is the likeness in their head structures. Where the embryology is known, the entognathy comes about through the formation of two plicae orales uniting at or below the sides of the labium. At the same time a change in the relative position of the mandibles and maxillae may take place, indicating an ingrowth of these mouth parts into the head, in which the mandibles may reach even to the hindmost part. From these changes a prognathous head results from a hypognathous one in so far as the functional mouth—the opening of the atrium—is directed forward, though the real mouth, the opening of the pharynx, is still directed downward. In connection with this prognathy stands the fact that the prosternum more and more overgrows the underside of the head, mostly so in Protura, where nearly half of the head is covered. This again, in Protura, involves a displacement of the forelegs, which take over the function of the antennae, as the latter become reduced to small organs with unknown function, if any—the pseudoculi.

A cavity on each side results from the coalescence of the plicae orales with the labium, which latter again, being pushed forward, coalesces more or less with the underside of the head, leaving only the hypopharynx (lingua and superlinguae) free, or the place where the hypopharynx should be if it is lacking (Protura). A fold from the plicae orales may grow in between the mandibles and the maxillae, resulting in two more or less definite cavities on each side, the gnathal pouches. Probably as stiffenings in the gnathal pouches, a skeleton is

formed, the fulcrum, which develops independently of the hypopharynx and takes on a curiously similar shape in all three groups, a V or Y basally biramously branched, and carrying some of the muscles of the maxillae.

The mandibles and maxillae are hollow at their inner sides; and into the cavities are inserted some of the adductor muscles that meet the corresponding ones from the opposite side or run to the fulcrum. In Protura the mandibles are for piercing, not biting, and having no use for adductor muscles, change them into protractor muscles and are solid, not hollow, inside. This is most probably a secondary phenomenon. Collembolids with piercing mandibles do not show these changes. A cardo is present and similar in all three groups, connecting the stipes with the fulcrum and running more or less parallel to, and dorsal of, the lateral branch of this skeleton. Snodgrass (1951, p. 84) expressly remarks that "the articulation of the cardo on the sternal brachium is in striking contrast to the usual suspension of the insect maxilla from the edge of the cranium." I have for practical reasons followed the common use in calling this rod the cardo, but in fact I suspect it to be actually a part of the fulcrum (to which it is attached by a ligament); in this case the so-called stipes would arise from a coalescence of stipes and cardo, and the maxilla would be located in the head in the same way as the mandible. It is also to be noted that at least in Collembola (fig. 11) a ligament connects the base of the stipes to the head wall in the same way as the mandible, and that the gnathal pouch does not seem to include the so-called cardo.

Now, if we want to test these characters, common to the three groups, according to their degree of relationship to other groups, as Hennig (1953) has schematized it (synapomorph characters being *derived* characters common to two or more groups, and symplesiomorph characters being only common inheritance) we find that the entognathy in itself is a synapomorphic character, being found in no other arthropod group. Also the shape of the fulcrum is a synapomorphic character, being not comparable to the ventral skeleton of the gnathal segments of malacostracan Crustacea, though it may bear some likeness to this. That the mouth parts are hollow at the median side is a feature they have in common with many myriapods, with which there is also a likeness in the shape of the mandible. On the other hand the shape of the maxillae is a true insectan character. The musculature of the mandibles suggests that of myriapodan groups, though no intrinsic muscles are found; an intermandibular muscle is found in Machilidae, but in no insect with doubly articulated mandibles.

bles. On the other hand the musculature of the maxillae is distinctly in accordance with that of pterygote insects, the tentorium having taken over the role of the fulcrum. There are also likenesses to the maxillae in Symphyla (Tiegs, 1940, p. 164), but in no other myriapodan group.

The symplesiomorph characters thus suggest relationship to both Myriapoda and Insecta. As to the synapomorph characters, it must be a matter of opinion whether one will regard them as indicating relationship, but it seems to me that the similarity in the way entognathy is brought about and the shape it has taken in the three groups is so great that it must involve a monophyletic origin. The shape of the gnathal pouches, the shape of the fulcrum, and the shape also of the mandibles and maxillae—the former suggesting Myriapoda, the latter Insecta and Symphyla—are so similar in the three groups that only a most curious coincidence would cause these characters to appear simultaneously in three independent cases.

I think, therefore, that the relationship between the three groups of entognathous apterygotes is much closer than between them and any other group, and quite certainly closer than between Diplura and Thysanura, or between Diplura and Symphyla. So, if entomologists want to remove Collembola and Protura from Insecta they must take Diplura with them; one cannot find in the Diplura any link to the "Insecta" and therefore neither do they support the theory of the symphylian origin of insects. To me it seems that all three groups taken as a unit have a distinct relationship to both Myriapoda and to Insecta, but form a branch of their own parallel to these; because of their hexapodan condition they may well be treated in entomological textbooks, but they do not represent "primitive insects" and they should not be treated together with Thysanura as "primitively wingless insects," because their relation to Thysanura is not greater than to many other arthropod groups. Perhaps it would be most convenient to follow Hennig (1953) and treat them together as a class of their own: Entognatha.

ABBREVIATIONS USED ON THE FIGURES

<i>ant</i> , antenna.	<i>gnP</i> , gnathal pouch.
<i>cd</i> , cardo.	<i>hph</i> , hypopharynx.
<i>dA</i> , so-called dorsal arms.	<i>lb</i> , labium.
<i>eph</i> , epipharynx.	<i>lbr</i> , labrum.
<i>fi</i> , filamento di sostegno.	<i>lc</i> , lacinia.
<i>fu</i> , fulcrum.	<i>lin</i> , lingua.
<i>ga</i> , galea.	<i>mcR</i> , midcranial ridge.

<i>mdb</i> , mandible.	<i>pro</i> , prostheca.
<i>mdbLg</i> , mandibulary ligament.	<i>ps</i> , pseudoculus.
<i>mLc</i> , ligament for the lacinia muscle.	<i>r</i> , rostrum.
<i>mx</i> , maxilla.	<i>st I</i> , prosternum.
<i>mxLg</i> , maxillary ligament.	<i>stp</i> , stipes.
<i>ph</i> , pharynx.	<i>su</i> , superlinguae.
<i>plp</i> , maxillary palpus.	<i>th I</i> , prothorax.

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