

The Snodgrass Tapes Evolution of the Arthropods

The third of three lectures by the insect morphologist Robert Evans Snodgrass delivered to the Department of Entomology at the University of Maryland in 1960.

Transcribed, assembled and annotated by Jeffrey W. Shultz

Robert Evans Snodgrass

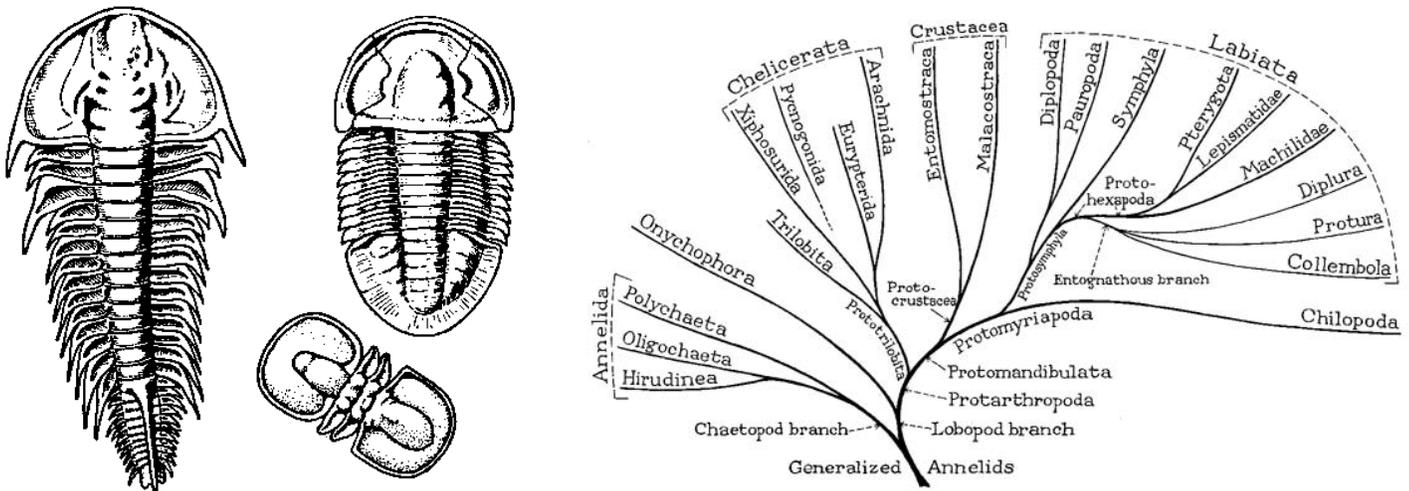
Well, the subject today will be the evolution of the arthropods. But, of course, I'll have to admit to begin with that I don't really know the truth of the matter. So, judging from what facts you can get together... I suppose at the present time that all evolution is accepted as a fact by all zoologists. And apparently the fundamentalists have given up trying to do anything about it. Yet it is a theory. And ... But it seems the idea of natural selection well-enough accounts for the physical evolution of animals; that is, certain genes produce the proper variations. But what bothers me about the ... about the evolution of the animals is how did the animal ever become such a complex assemblage of chemical substances.

I've had a cold, but I guess I can talk through it.

Every cell in the body, for example, has to have its own enzymes to do its work it's supposed to do. And all these activities have to be correlated and regulated by hormones, and hormones, again, are just chemical compounds. And, so, it seems to me that that's one of the problems of evolution yet is to find out how all of these chemical substances ever got together in the animal in the proper amount, in the proper places and [how they came] to do the things that they do do.... and how the biochemicals do all the things they do... [1]. Well... We don't have to ... in morphology, we don't have to worry about those subjects, but still it's something to think about. But once the animal, of course, is a working machine, chemical working machine, why then, natural selection can carry on.

? ... again, say, the evolution of a particular animal or a group of animals they have to start with the forms already organized. And wherever there are fossils available, the paleontologist can get some evidence of the actual evolution the animal's gone through. For example, there's apparently little doubt that birds are derived from reptiles, and the evolution of the horse is pretty well worked out from the fossils, but those are exceptional cases. And even in our own evolution from some kind of an ape, it is pretty well attested by the fossils of ancient men that they now know of ... carry them back to primitive men then to ape men and then apes and so on. So we can hardly deny our own evolution from the evidence of the facts that are known. In fact, the paleont... the anthropologists now have a fossil that they can't tell whether it's a man or an ape... where to put ... where to classify that. Well, our own evolution goes back to about a million years to the ice age of the Pleistocene, but the arthropods, on the other hand, were well developed and differentiated way back in the Cambrian and that was 500 million years ago [2], according to modern way of reckoning time.

Figure 1



Representative Trilobites

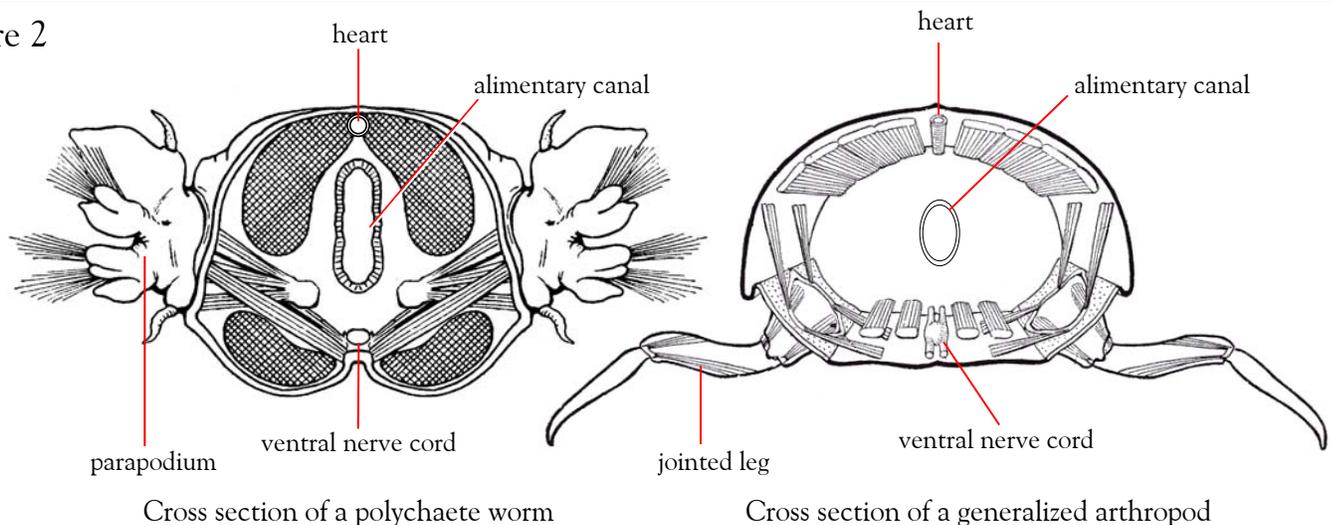
Phylogenetic tree of Arthropoda proposed by Snodgrass in 1938.

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And we all know the trilobites, of course, but along with the trilobites there were plenty of fossil forms of different kinds of arthropods living at the same time [3]. And even the trilobite, you see, is a highly specialized animal. It's generalized in that all of its appendages are legs, locomotory legs, but otherwise it's highly specialized. And it would be a long stretch from an amoeba to a trilobite in evolution. And the evolution of a spider from a trilobite would be a relatively simple matter. So, the evolution of the arthropods must have begun way back in Precambrian times, and geologists, most ... some of them, think that the Precambrian was as long in duration as all the time since then [4]. So ... (Aside: See you when I get to go.) ... and another thing there are no fossils preserved in the Precambrian [5], so here, we just have free ... give free rein to our imagination. But there are certain facts from the modern arthropods we know that can be utilized in getting some kind of an idea. But then you must always remember that phylogenetic trees are pretty imaginary ... or ... because... we've got in entomology a whole forest of phylogenetic trees now; they're all different and each fellow that makes a tree has it branching out in different ways from the other fellow that went before him. So, you can't rely very implicitly on the reconstruction of phylogeny. But some will be more plausible than others, and that's the best we can do [6]. But even the vertebrates have been theorized very extensively as to their origin. I've read three different accounts of the origin of the vertebrates in the last year, and they're all totally different. And one of them even has the vertebrates originating from arthropods [7]. And each fellow, I suppose, is convinced of this own ideas, but he doesn't convince [the] others.

Figure 2



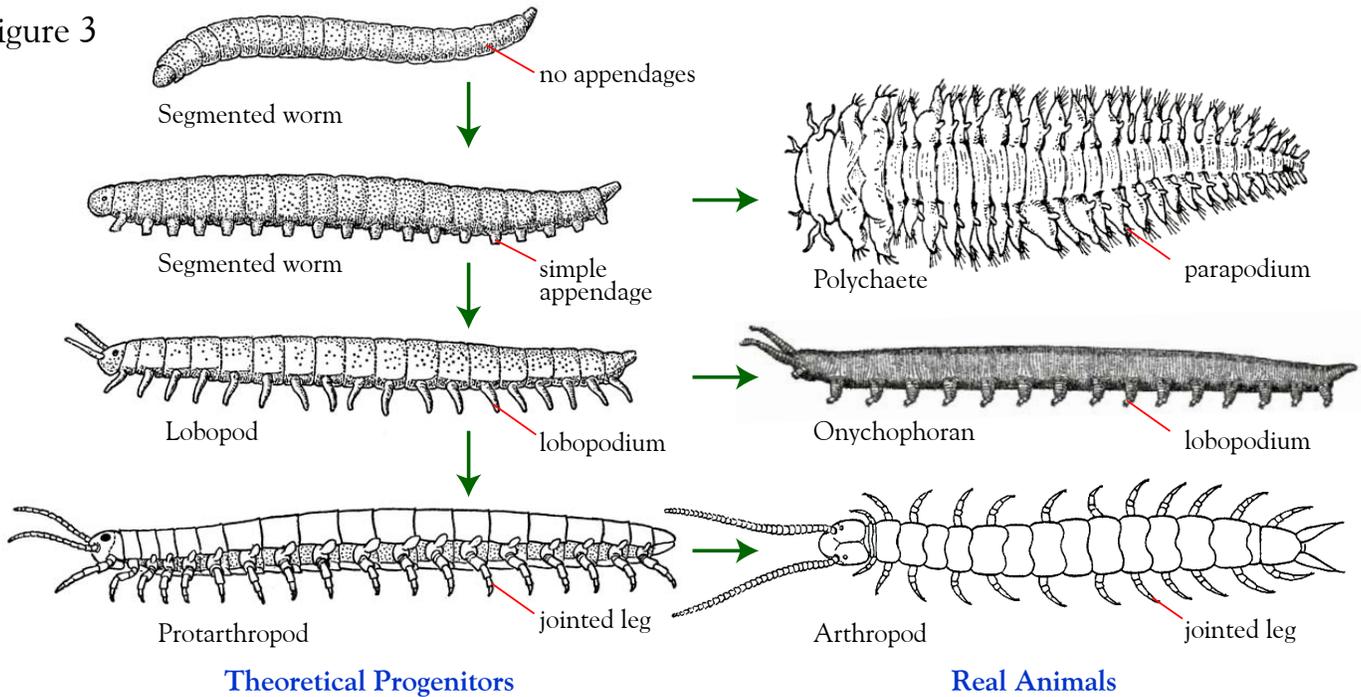
Well, now a long-standing theory concerning the origin of the arthropods is that they have been evolved from polychaete worms [8]. You know what a polychaete worm is, I suppose. It's one of those ocean worms that has flaps along the side of the body ... that is used for locomotion. And I suppose the presence of these flaps, called parapodia, is the reason... the principal reason why the polychaetes have been picked out to be the origin ... the ancestors or progenitors of the arthropods. But if you look at the two, you see they're entirely different. For example, the cross section of a worm just roughly would be something like this. Along here on the side would be a ... bilobed flap ... [It's] a more complicated structure than that, but that's good enough ... And coming from those [we have] ... a few bristles. ???... along the side of its body, but these have more and they're longer. But now compare that with a similar section of an arthropod. Why, it's entirely different. Here are the leg's coming off down here ... [In the polychaete], then, there are lateral flaps with no resemblance to legs, the true jointed legs of an arthropod. [The polychaete parapodia are] lateral; [arthropod legs are] ventral. Now, moreover, there's a long spine that comes out like that, each one of these groups of bristles, and most of them attached to that to the bristles. So, down here, the arthropod's legs will come ... come from the body. So, you see there's no similarity, then, between the two animals at all, that I can see ... or that anybody can see, for that matter. But, of course, they do have the same fundamental organization -- the alimentary canal in the middle, ventral nervous system, dorsal circulatory system and all that. So, there's no doubt that the polychaetes and the arthropods are fundamentally related, but they have to be related to each other not directly, but through some long extinct ancestor, common ancestor [9]. And, of course, the polychaetes are just one group of the ... of the annelids -- worms -- which includes the earthworm and leeches. So, I would dispose of that idea, simply because there's not enough resemblance between the two in their actual mechanical operations [and] structure. The fact that they've got .. each of them have an alimentary canal and a nervous sytem, a heart, well you've got to have those things, anyway ... And then another thing, the polychaetes,

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you see, are highly specialized worms, and it's not usually supposed that one specialized animal gives origin to another specialized type of animal. You have to go back to something that they had in common. Well, recently a man has described a fossil polychaete from the Cambrian. Well, as I've just said, the origin of the arthropods must have been way back in the Precambrian, millions of years, so there's no evidence whatever that there were any polychaetes in existence at that time. And, as I say ... as I said, there are no fossils preserved from the Precambrian; they've all been destroyed.

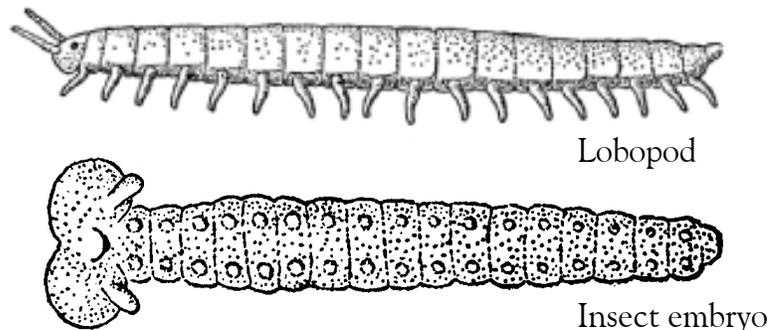
Figure 3



Evolutionary origin of arthropods inferred by Snodgrass based on comparative anatomy and embryology. Snodgrass postulated that the lobopod stage corresponds to the embryo of arthropods and onychophorans.

Well, the adult arthropod, of course, doesn't give you any idea as to how it began, but the embryo, seems to me, gives you some very good ideas of how the arthropods must have begun from worm-like progenitors. Of course, it's become the fashion in recent years to discredit the embryo with repeating its life [evolutionary] history, [10] well it doesn't in all cases, of course; it can't. Because being shut up in an egg shell is a very different way of living from the free-living animal that gets its food from the outside. The embryo, you see, has its food in the form of yolk, yolk stored within its body. And so, it has to form this alimentary canal by the stomach growing around and enclosing the yolk. Well that, of course, can't be recapitulation. But that's just one case. But now you take the ... embryo stretched out on the underside of the egg. As I said before, it has this head up here and a long body that becomes segmented ... And on each one of those segments, a couple of ... a pair of small lobes grow out ... and become the various appendages ... mouthparts, legs, swimming appendages, whatever kind of appendages may develop. Antennae going up in here, mouth would be located there.

Figure 4

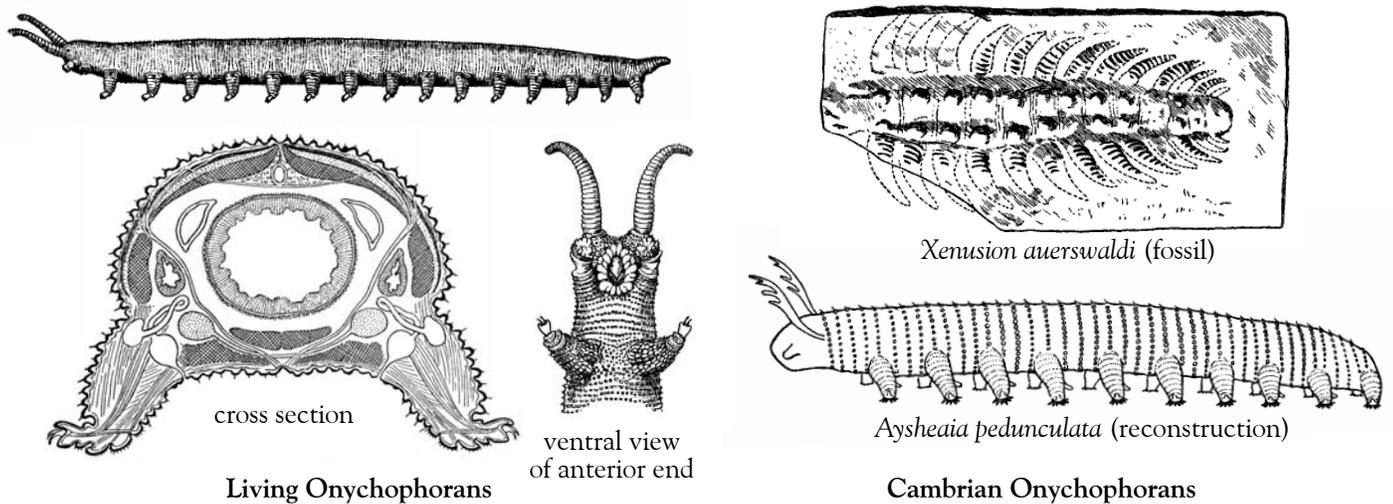


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Well, now, since the embryo of all the arthropods begin that way... Well, there may be exceptions that skip over an early stage, but most of them don't. And even the onychophorans, the early embryo is like that. That is to say, it has a series of lobe-like rudiments of appendages on the under side. Well, so, why cannot that stage of the embryo, then, be taken as the beginning of the evolution of the arthropods from a worm-like animal. For example, if you translate that embryo into a worm ... and then give it a small lobe-like outgrowth up here on the underside of each segment. You can have something that certainly seems possible that it could have developed into an arthropod. Well, of course, now, that's ... this is an actual fact, as I say, with all the arthropods and the onychophorans. But this creature here, of course, is imaginary ... ??? ... Now, if that represents the early stage of the development of the arthropods, why couldn't a thing like that represent an earliest stage in the evolution of the arthropods? Well, I call that a lobopod ... I don't know... I've had this idea in print, but I don't know if anybody's accepted it, because they're all so wedded to the theory that the arthropods came from polychaete worms. Now you have to assume, of course, that this had an ancestor of simpler form, just an ordinary segmented worm without any lobes down here ... as such. So, this would be an ordinary worm, segmented worm. But I suppose it had at that time, all the fundamental structure, internal organs, of the arthropods and the worms do have. So, that from that you might suppose that the annelids, gave off the bristleworms, develop by getting these bristles along the side that was developed in the polychaetes, and they formed an entirely separate branch from this primitive segmented but undifferentiated worm.

Figure 5



Onychophora: living and extinct

Well, now, the onychophoran *Peripatus* is just a highly developed lobopod. Suppose you take a cross section of the body ... You have those appendages there -- just a little bit bigger-- but since we have to suppose that the integument was soft, pliable, these things couldn't be developed into long segmented legs right away, and the onychophoran does the best it can with thick and short legs. Well, the Onychophora are known from way back in the Cambrian [11]. They differ very little from modern forms. Surely, the onychophoran hasn't been able to evolve into anything different. It can't, on account of its soft skin, and they've done all that they can by just enlarging their legs and getting some extra internal organs. So there, again, I'd say, that this is a highly developed lobopod. But you often see in the books and papers the idea that the onychophorans are the ancestors of the arthropods. But I don't believe it at all; they're simply an offshoot of this polypod [or] lobopod, rather, and they haven't evolved into anything else in all these millions of years. So, it's very unlikely that they could be the ancestors or progenitors of the arthropods.

Well, then, what we've got to assume is... Now you see the difference ... what's characteristic of the arthropods is their hard external skeleton; that's what has made them what they are. Well, then, we'll suppose that from this lobopod ... soft-bodied lobopod worm ... another line of evolution was differentiated by the hardening of the cuticle, sclerotization of the cuticle. Then, with the muscles already attached on the cuticle, why it opened up no end of possibilities for mechanical modifications. In the first place, these legs could become longer and slenderer ... and, finally, they could become jointed. Well, just recently I've learned that there is ... there are some

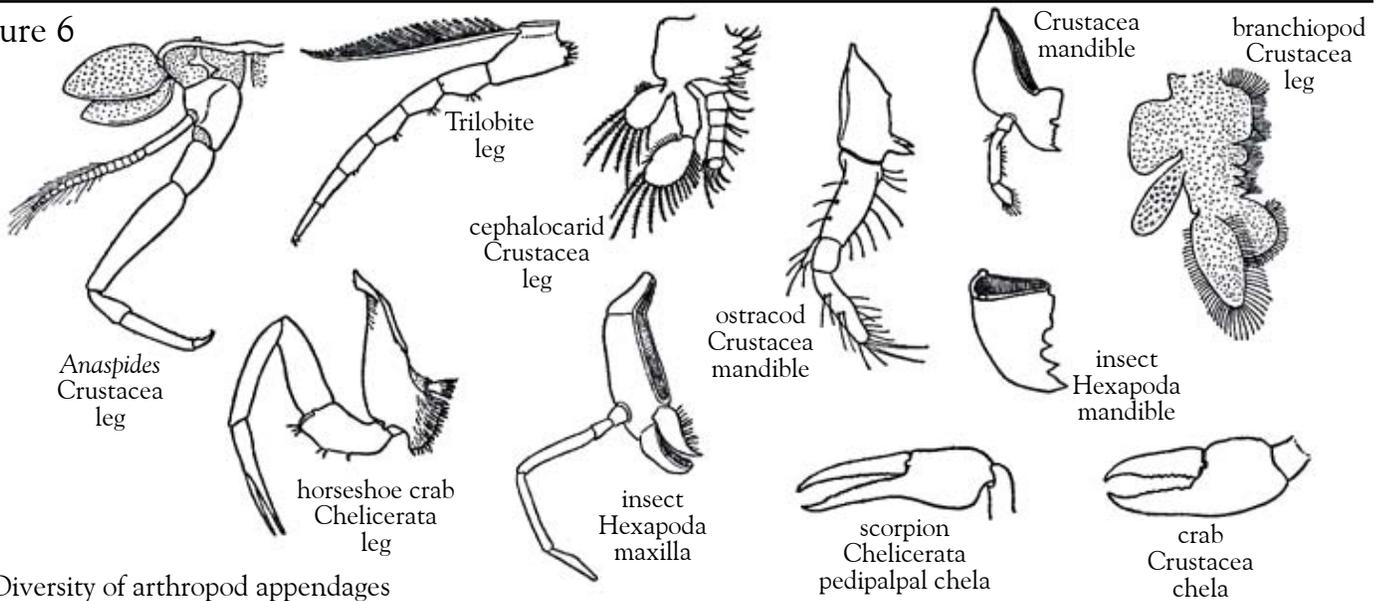
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specimens of Cambrian arthropods in the National Museum that do have legs exactly like that -- just long, slender, unjointed appendages -- but they can't be certain what the animals are because the front end here is broken off of all of them [12]. But, anyway, it does give ... a good representation of this thing in the center, where the appendages are just long, slender, unjointed processes. But, now, with the proper ... the sclerotization of the integument, why you see you've got on the back the plates here, and then from that the leg becomes longer, jointed, segmented. So, it seems to me that that's the most reasonable idea which you can get of how the arthropods began. That lobe-pod we have down there, we can call a progenitor of the arthropods but not the ancestor, because the arthropod by definition has to have jointed legs. But, you see, with the muscles attached on this skeleton, there's no end to the possibilities of mechanical development, and that's what the arthropods are noted for, the skeletomuscular mechanisms that they develop, as no other animal can that doesn't have a hard external skeleton.

Well, now, I might note now that the term ... we used the term "sclerotized" for the hardening of the cuticle. We used to say that it was strongly chitinized, but we know now that the hardened part is not chitin but a protein. But just recently I saw a paper ... read a paper in which the writer spoke of the strongly sclerotized parts ... I mean, strongly chitinized parts of the skeleton. It's just out of date is all.

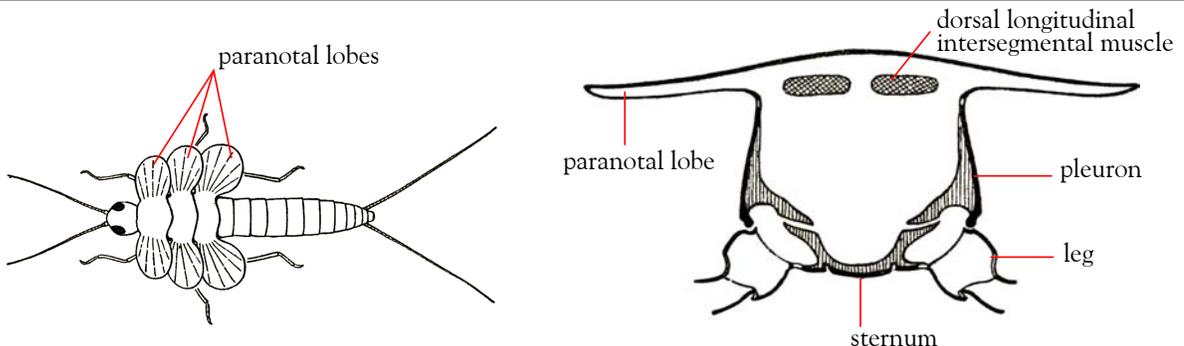
Figure 6



Diversity of arthropod appendages

Well, the arthropods, anyway, you see, have so many legs. I mean, in that stage, that they didn't need them all to walk, so they ... some of them have been converted into various other organs for other purposes. As I explained the last time, the mouthparts are all simply modified legs, and, then, of course, some of them kept the legs for locomotion, others have become swimming organs and others have become implements of various purposes. And the arthropods are the most diversified of all animals on account of their structure. The vertebrates with its bones inside of the body can't have as many mechanical modifications as the arthropod with their muscles attached to a hard skin.

Figure 7



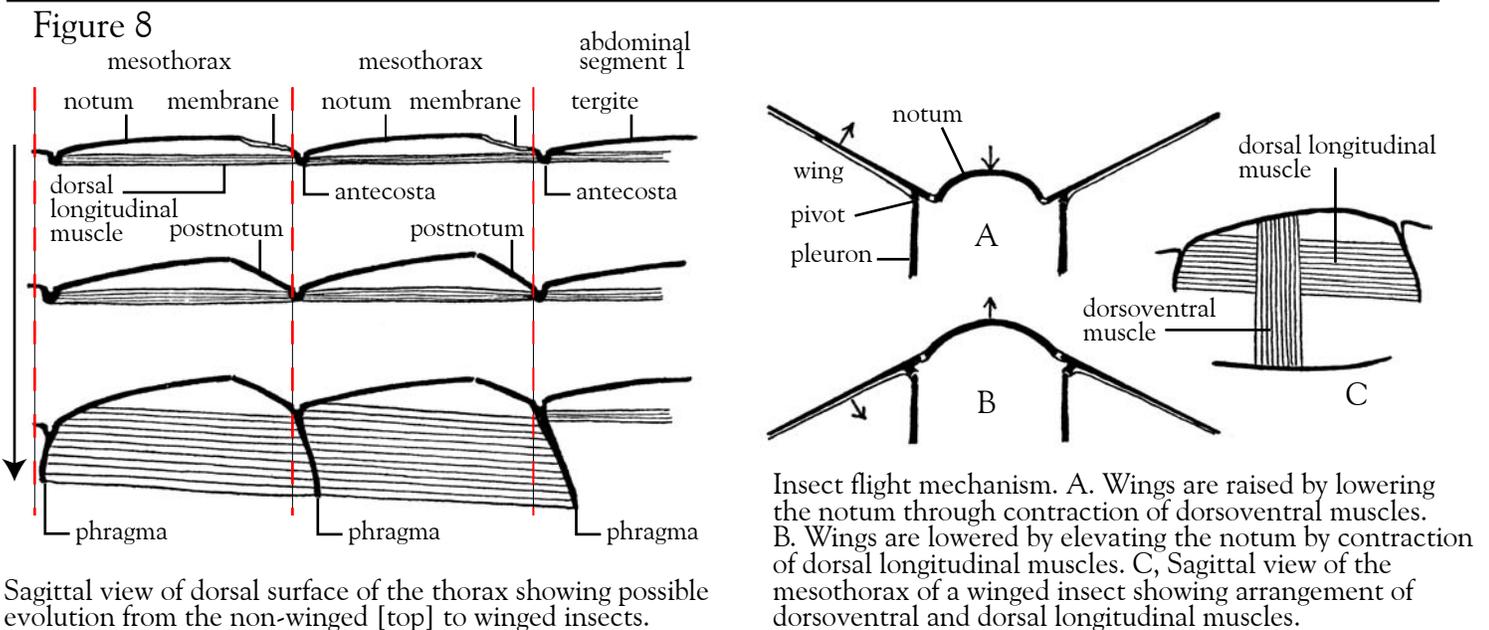
A suggestion of possible structure of a primitive insect with three pairs of paranotal lobes that may have been used in gliding.

Theoretical diagrammatic cross section through a thoracic segment of a hypothetical insect with paranotal lobes in place of wings.

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Well, then, finally, of course, the insects were able to develop wings, stiff, flat outgrowths of the back [13], which no other animal has done, no other real animal. Well, you see, the other animals that have developed wings, like the ancient reptiles ... winged reptiles, modern bats and birds, they all had to use a pair of their front limbs, convert them into wings. And then they have to get along as best they can with one pair of legs. But the insects have had the advantage that they could have wings and keep all their legs. Well in that respect, of course, the insects resemble the ancient winged dragons and the winged horse Pegasus. But, as I said, the inventors of those animals were not anatomists; they didn't explain how those animals could move their wings. Well, of course, finally, I should note that in the same class anatomically are the angels and the devil. Well, I've always been much puzzled to know how they could move their wings. Well, I shouldn't want to meet Satan personally, but I should make it into heaven some time just to be able to study the wing mechanism of an angel. But I don't suppose I'll ever get there. But, anyway, it's a puzzle to think about. Because the birds, now, you see, have to have that enormous breast bone and those greatly developed chest muscles in order to move their wings. Well, ... some things we'll never know, of course.



But it would be interesting to diverge and see what the insects had ... what modifications the insects had to do ... go through in order to move the wings after they got the wings in the form of lobes growing out of the back ... Take the ordinary succession of segments ... I suppose those would be the back ... that would be the back of an insect without wings ... but with that muscle ... ??? ... that ingrowth there, there's a cross ridge [antecosta] ... that lets the muscles go from there to there ... But the whole back, you see, is not sclerotized. You see the back plate [notum] has about that much space between each of those segments and then this part of the segment is membranous, but the real line ... lines of division between the segments are these ridges to which the muscles are attached. Well, now, we call that the intersegmental membrane, but, you see, it isn't that at all. It's the posterior part... the unsclerotized posterior part of the segment, and when those muscles contract why they simply pull those segments together. And the membranes go ... membrane folds in like that. So, well, that would never do for a wing mechanism, so the insects that have wings have avoided that ... ??? ... Well, this is the back of a winged segment ... there is a great... ??? ... [dorsal] longitudinal muscles and then there are others [dorsoventral muscles] that go from the back down this way. So, the alternative contraction of those two sets of muscles that move the wing up and down [14].

When these muscles ... maybe I should have made ... ??? ... when these muscles ... lengthwise muscles contract, why the back goes up and when these [dorsoventral muscles] contract it pulls it down. So that the... When it [back] goes up, you see, the wings go down and when this [back] comes down -- there would be a pivot right here -- so that would make the wing go up ... Well, they had to develop that ... something there to prevent locomotor ... this pulling of the segments together [and this is provided by] the sclerotization of that membrane. So, in that case you see ... ??? But from that results ... from that results the fact that the back of the membrane, the segment is composed of two parts. This we call the notum and this part the postnotum. So, you see, that's a device, then,

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for preventing the infolding of the segments into each other by sclerotizing the posterior membrane. And that's characteristic of all the wing-bearing segments of the insects, that there are those two plates in it. Well, the muscles have to be enlarged, of course, so ... and get these great phragmata in there ... ??? ... like that. Well, the insects had to go through that much modification at least before they could move their wings. And it is supposed that their wings were first flat outgrowths of the back called paranotal lobes that enabled them to glide [15]... and then this modification. But, then, of course, also, the pleuron had to be modified, stiffened, sclerotized in order to support the wings from below.

How much more time do I have?

William Bickley: About five minutes.

Snodgrass: Five minutes. Well, perhaps I've said enough. Are there any questions about any of these lectures?

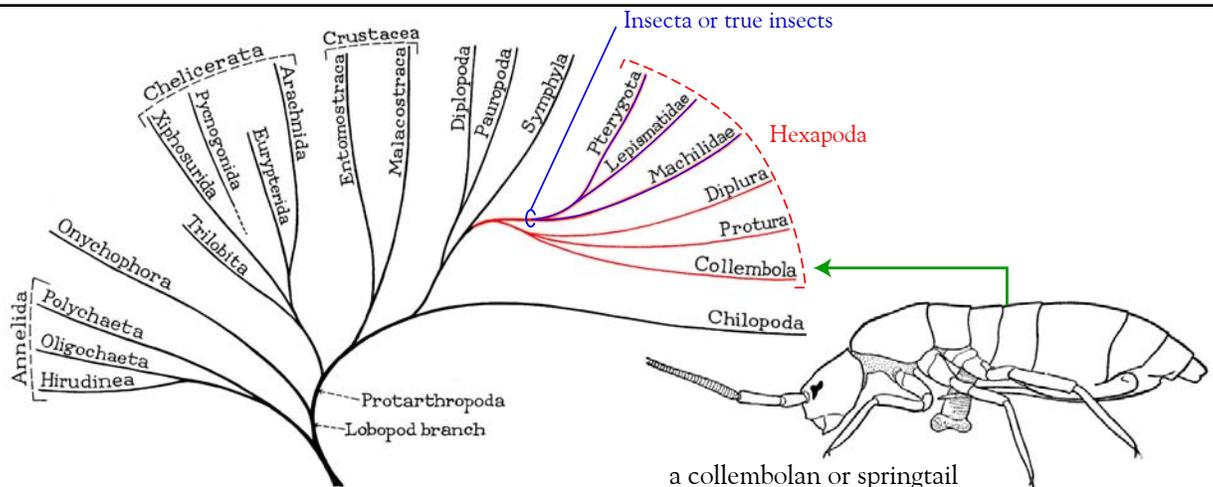
Questioner 1: You have no particular theories for the forward and rotating motion?

Snodgrass: Oh, no. Of course, that has to be... The up and down flapping of the wing wouldn't produce flight; you'd have to have the rotary movement [16]. Well, that's provided for by special muscles that attach on the base of the wing. And, so, they didn't get their wing ... wings all at once, you see. They got ... probably got these paranotal lobes that enabled them to glide and then they had to go through considerable evolution to make them work as locomotor organs in the air. But, certainly, they have perfected that mechanism. There's no better fliers, even airplanes, than an insect.

Questioner 2: What is wrong with the concept that a mutation could occur in a highly specialized animal to give rise to another highly specialized ...? What's... It's already gone too far? I don't see why the germ cells couldn't be modified to give rise to something different ... maybe not a great deal different. But then you have a subsequent mutation, you could get something quite different.

Snodgrass: Yes, I don't understand the genetic idea about mutations very well, because suppose you did get a favorable mutation that makes something useful, but suppose that that part has to cooperate [or] work with some other part. Well, the two have to be modified in different ways but in ways that will work together. And how long does the animal have to wait between mutations for favorable changes to come about? So, the whole business of how evolution has taken place is still sort a mystery to me. And, well, so many mechanisms, you know, in the insect that require a whole lot of parts to work together.

Figure 9

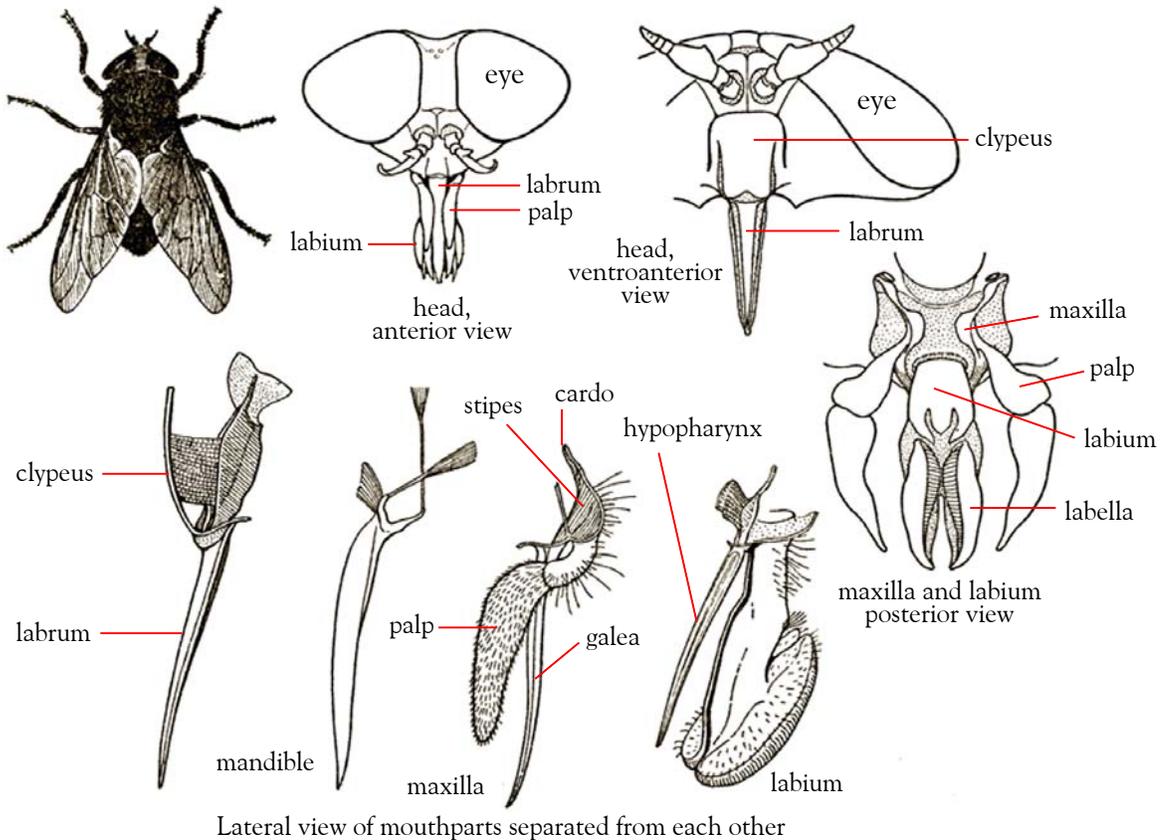


Phylogeny proposed by Snodgrass (1938). Hexapoda is now widely considered a group of terrestrial crustaceans.

Snodgrass: Well, that depends on what the definition... But, yes, they ought to be insects ... hexapods, anyway. If you don't want to use "insects", you can just call them hexapods. That's because, you see, they're more related more to the thysanurans and pterygotes than to anything else. But, of course, there are some who claim they are not insects, but that's just a matter of definition. So, I usually get around that by calling them all hexapods [17].

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Figure 10



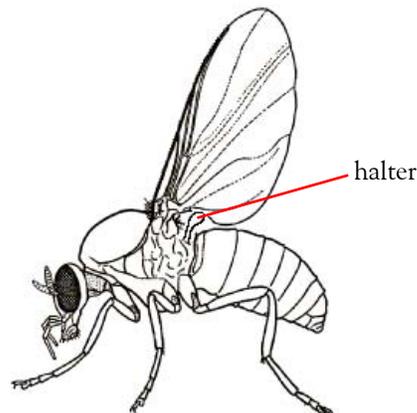
Head and mouthparts of a horse fly, *Tabanus atratus*, showing complexity of the piercing-sucking mechanism

Snodgrass: Well, I was going to say, now, the mechanism of the mouth ... of the sucking mouthparts of the insects can be extremely complicated in that it involves a modification of a lot of different parts so that it will all work together. And how all that came about is, as I say, mystifies me. Because in experiments on *Drosophila*, they don't get very many mutations that are useful; they all seem to be harmful, some of them. And so it must be a long time between mutations that are useful, when some half a dozen things all have to be modified so as they'll work together as a unified mechanism. Well, then, the problem becomes how to achieve it.

Anything else?

Bickley: In the Diptera, the halteres are they... They are rudiments are they not?

Figure 11



A black fly, *Simulium venustum*, showing modification of hind wing into a halter

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Snodgrass: Well, as I said ... as I explained last time, a rudiment is something that's going to grow up to be something; a vestige is something that has gone backward. Why, yes, I believe undoubtedly, the halteres are reduced wings. I don't think there's any question about that. But they've become useful in quite a different way. They're now regarded ... sense organs in them ... they've become organs of equilibrium.

Well, of course, this ... I haven't, by any means, covered the whole subject, but I've explained that a lot of variations have taken place to make the arthropods what they are as a group.

BELL

Bickley: Thank you very much.

APPLAUSE

Snodgrass: You don't have to believe any of this stuff ...

NOTES

1. Snodgrass elaborated somewhat on this topic in one of his last papers, which was published posthumously.

Snodgrass, R.E. 1963. Some mysteries of life and existence. *Annual Report of the Board of Regents of the Smithsonian Institution, 1962*. United States Government Printing Office: Washington, D.C.

2. The Cambrian Period is currently thought to have begun about 550 million years ago and to have ended about 490 million years ago. For a geological time scale go to the web site of The Geological Society of America (<http://www.geosociety.org/science/timescale/timescl.htm>).

3. The number of known Cambrian arthropods and lobopods has increased substantially since 1960, at which time only the Burgess Shale Fauna of British Columbia was widely known. Other important Cambrian fossil-bearing deposits now include the Chengjiang Fauna of China and the Orsten Fauna of Sweden. These deposits are remarkable for the detail of preservation which sometimes includes the soft anatomy. For a list of such deposits or *Lagerstätten*, go to Fossil Lagerstätten (Univ of Bristol) and The Dawn of Ocean Life Exhibit

4. Earth is estimated to be 4 billion years old and the Cambrian began about 550 million years ago. So, the Precambrian persisted for about 3.5 billion years.

5. Precambrian fossils are known, such as the Ediacaran Biota of the Ediacara Hills in Australia (Vendian Period, 540-650 million years ago), but the life forms are typically very different from those of the Cambrian and only a few would seem to resemble annelids, lobopods or arthropods, such as *Dickinsonia* and *Spriggina*. Similar fossils have been found in Russia, Canada and Namibia.

6. In Snodgrass's time, alternative phylogenetic trees were evaluated by their relative "plausibility." Snodgrass recognized that plausibility was a rather ill-defined and subjective criterion, as indicated by his closing statement. In practice, plausibility was the believability and consistency of the evolutionary story the phylogeny told. For example, Snodgrass rejected the idea that polychaetes were the ancestors of arthropods, because the parapodia did not seem to him to be capable of generating the jointed appendages of arthropods. This argument makes many implicit assumptions about function, development and evolution. Dissatisfaction with this approach eventually led to more objective and explicit criteria for generating phylogenetic hypotheses. This includes parsimony, which favors the phylogenetic hypothesis that minimizes the number of convergences and parallelisms in evolution, and maximum likelihood, which favors the phylogenetic hypothesis that is most likely or probable given a probabilistic model of evolution. Despite these advances, however, there is still "a forest of phylogenetic trees."

7. Snodgrass is probably referring here to the work of William Patten (1861-1932), who proposed the origin of vertebrates from arthropods similar to horseshoe crab, *Limulus*. The idea required a convoluted scenario and never received much support and is now only of historical interest. Patten developed his idea most thoroughly in

Patten, W. 1912. *The Evolution of the Vertebrates and their Kin*. P. Blakiston's Sons, Philadelphia.

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NOTES

8. Since the late 18th century, biologists assumed that the similarities of annelids and arthropods (*i.e.*, segmented bodies, mesodermally derived osmoregulatory organs, dorsal artery, ventral nerve cord, development by posterior addition of somites, *etc.*) reflect a close phylogenetic relationship and were combined in a group called Articulata. The morphology of onychophorans or velvet worms (*e.g.*, *Peripatus*) seemed intermediate between annelids and arthropods, and thus strengthened the Articulata concept. However, recent studies of molecular sequence data, especially from 18S ribosomal nucleotides, indicate that arthropods and onychophorans are more closely related to such invertebrate phyla as Kinorhyncha, Tardigrada and Nematoda and are only distantly related to Annelida (Aguinaldo *et al.*, 1997; Halanych, 2004). Arthropods and their relatives were then placed in a group called Ecdysozoa, which is united, in part, by absence of cells with ciliary motility and by presence of a chitinous cuticle and growth through molting or ecdysis. The Ecdysozoa concept rapidly achieved wide acceptance and support for Articulata faded (but see Nielsen, 2001), such that many zoologists would now regard Snodgrass' emphasis on annelid-arthropod similarities to be outdated. However, the morphological similarities of Annelida and Arthropoda remain and require explanation, regardless of the phylogenetic proximity of the two phyla. If Ecdysozoa is real, then annelid-arthropod similarities are either remarkable parallelisms or reflect a shared ancient body plan that was lost many times among the ecdysozoans or both, perhaps in association with reduced size or simplifications caused by altered ecology. Any scenario has significant implications for understanding evolutionary factors governing long-term changes in body plans, the origin of phyla and the role of morphology in phylogenetic analysis. We are not yet in a position to say that Snodgrass' and other workers were right or wrong in looking to annelids in their attempts to understand arthropod evolution.

Aguinaldo, A.M.A., J.M. Turbeville, L.S. Linford, M.C. Rivera, J.R. Garey, R.A. Raff & J.A. Lake. 1997. Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature*, 387: 489-493.

Halanych, K. 2004. The new view of animal phylogeny. *Annual Review of Ecology, Evolution, and Systematics*, 35: 229-256.

Nielsen, C. 2003. Proposing a solution to the Articulata-Ecdysozoa controversy. *Zoologica Scripta*, 32: 475-82.

9. Snodgrass is referring here to the Haeckel's Biogenetic Law or "ontogeny recapitulates phylogeny." He clearly rejected the view that stages of embryonic development literally reflect ancestral forms, but it is also evident that he felt that embryos recapitulated evolution in a significant way. Because development is a morphological transformation that can be observed and described as rigorously as the anatomy adult insect, generations of biologists have been seduced into using development as a kind of surrogate for evolution. Snodgrass was a member of such a generation. Despite Snodgrass' fact-theory dichotomy, his thinking was clearly guided to a large extent by an implicit "theory" of recapitulation. See Gould (1977) for a classic treatment of the recapitulation issue.

Gould, S.J. 1977. *Ontogeny and Phylogeny*. Belknap Books, New York.

10. A wide variety of Cambrian lobopods are known and continue to be discovered. Snodgrass was familiar with those of the Burgess Shale, including *Aysheaia* and *Xenusion*. Important lobopods have emerged from the Chengjiang deposits, including ones with dorsal spines and sclerites (*Microdictyon*) and annulated legs.

11. Snodgrass is probably referring here to the Burgess Shale lobopod *Hallucigenia* that was originally reconstructed upside-down. The long, unsegmented legs that Snodgrass refers to are actually long dorsal spines. For additional details see The *Hallucigenia* Flip (http://gsc.nrcan.gc.ca/paleochron/09_e.php).

12. Paranota are lateral extensions of the thoracic nota present in some fossil and living arthropods. There is a long-standing hypothesis that wings evolved through the elongation of paranotal lobes and that they were first used in gliding, but this idea was questioned when it was found that paranota do not generate significant lift until they are very long (Kingsolver & Koehl, 1985). Consequently, if small paranotal lobes experienced no selection for improved aerodynamic function, it is difficult to explain how the paranotal lobes got long enough to become aerodynamically effective. It was then suggested that long paranota were needed for some other function, such as thermal regulation, and only became airfoils when they reached a certain size. In contrast, developmental genetic work (Averof & Cohen, 1997) suggests that insect wings are homologous with gill branches (epipodites) of crustacean appendages and are not homologous to paranotal lobes.

Averof, M. & S.M. Cohen. 1997. Evolutionary origin of insect wings from ancestral gills. *Nature*, 385:627-630.

Kingsolver, J. G. & M.A. Koehl. 1985. Aerodynamics, thermoregulation, and the evolution of insect wings: differential scaling and evolutionary change. *Evolution*, 39: 488-504.

The Snodgrass Tapes

Lecture 3. Evolution of the Arthropods

NOTES

13. The model proposed by Snodgrass is apparently correct and widely accepted.

14. The gliding ancestor model for the origin of insect flight is closely tied to the paranotal theory for the origin of wings. Significantly, recent studies suggest that wings may have initially been used to propel aquatic insects as they stood on the water surface (*i.e.*, surface skimming), a behavior now used by emerging mayflies and stoneflies. [For more details, go to Jim Marden's web site on the Evolution of Insect Flight. (<http://www.bio.psu.edu/People/Faculty/Marden/project2.html>)] The connection to aquatic locomotion is interesting given evidence for the homology of wings and gills. [See 12].

15. The rotational movement of wings around their long axis has been shown to be critical for generating lift in insects. This mechanism was not anticipated by aeronautical engineers, who are generally concerned with the aerodynamics of fixed-wing aircraft.

16. The classification of Collembola (springtails) described by Snodgrass is still valid; they are hexapods, but not insects.

Figure Credits

Figure 1. Snodgrass, R.E. 1938. Evolution of the Annelida, Onychophora, and Arthropoda. *Smithsonian Miscellaneous Collections*, 97(6): 1-159, figs 36, 54.

Figure 2. Snodgrass, R.E. 1935. *Principles of Insect Morphology*. McGraw-Hill Book Co.: New York, figs 41, 42.

Figure 3. Snodgrass, R.E. 1958. Evolution of arthropod mechanisms. *Smithsonian Miscellaneous Collections*, 138(2): 1-77, figs 1, 2; Snodgrass, R.E. 1938. Evolution of the Annelida, Onychophora, and Arthropoda. *Smithsonian Miscellaneous Collections*, 97(6):1-159, figs 13, 52.

Figure 4. Snodgrass, R.E. 1958. Evolution of the Annelida, Onychophora, and Arthropoda. *Smithsonian Miscellaneous Collections*, 97(6): 1-159, fig. 21; Snodgrass, R.E. 1960. Facts and theories concerning the insect head. *Smithsonian Miscellaneous Collections*, 142(1): 1-61, fig. 1A.

Figure 5. Snodgrass, R.E. 1938. Evolution of the Annelida, Onychophora, and Arthropoda. *Smithsonian Miscellaneous Collections*, 97(6):1-159, figs 21, 29.

Figure 6. Snodgrass, R.E. 1958. Evolution of arthropod mechanisms. *Smithsonian Miscellaneous Collections*, 138(2): 1-77, fig.21.

Figure 7. Snodgrass, R.E. 1930. How insects fly. *Smithsonian Report for 1929*: 383-421, figs 3, 6.

Figure 8. Snodgrass, R.E. 1958. Evolution of arthropod mechanisms. *Smithsonian Miscellaneous Collections*, 138(2): 1-77, figs 23, 24.

Figure 9. Snodgrass, R.E. 1938. Evolution of the Annelida, Onychophora, and Arthropoda. *Smithsonian Miscellaneous Collections*, 97(6): 1-159, fig. 54; Snodgrass, R.E. 1935. *Principles of Insect Morphology*. McGraw-Hill Book Co.: New York, fig. 147.

Figure 10. Snodgrass, R.E. 1943. The feeding apparatus of biting and disease-carrying flies: a wartime contribution to medical entomology. *Smithsonian Miscellaneous Collections*, 104(1): 1-51, fig. 11.

Figure 11. Snodgrass, R.E. 1943. The feeding apparatus of biting and disease-carrying flies: a wartime contribution to medical entomology. *Smithsonian Miscellaneous Collections*, 104(1):1-51, fig. 9.