

The Snodgrass Tapes

Facts and Theories on the Insect Head. Part 1.

The first 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

Moderator: William Bickley, Chair, Department of Entomology, University of Maryland

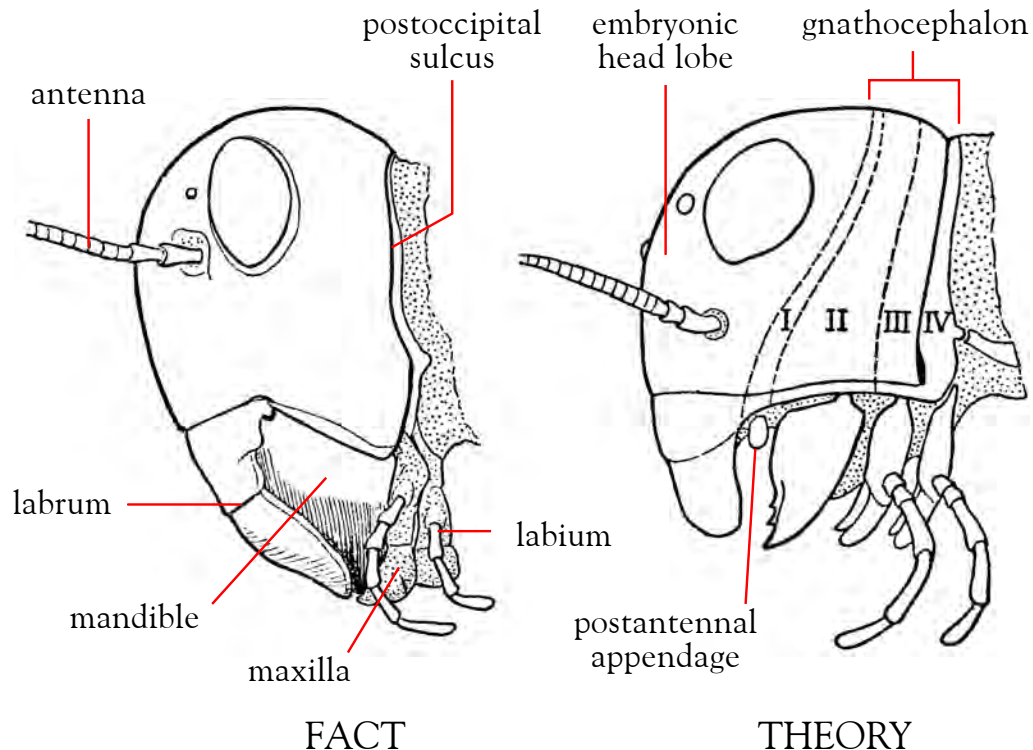
Bickley: ... here for two more Mondays, and today he's going to start on "Facts and Theories upon the Insect Head." He may continue that a little bit more next Monday... Dr. Snodgrass.

APPLAUSE

Robert Evans Snodgrass

I'm glad to see you all here. And ... this subject "The Facts and Theories on the Insect Head" is one that I may not be able finish up in one lecture, and, if so, I'll carry it over on to the next. But I had too many subjects that I had hoped to get around to. We might simplify the title "The Facts and Theories on the Insect Head" to a subject of the segmentation of the insect head. But that subject is mostly theoretical. There have been plenty of theories about it. And I can't tell you yet which theory is right and which is wrong, but I can ... I think I can show you what ... that some theories are ... are more plausible than others. That's about the best we can do with theories. Because theories, you see, are something we make up in our own minds. For the facts, we have to go to the insects [1].

Figure 1

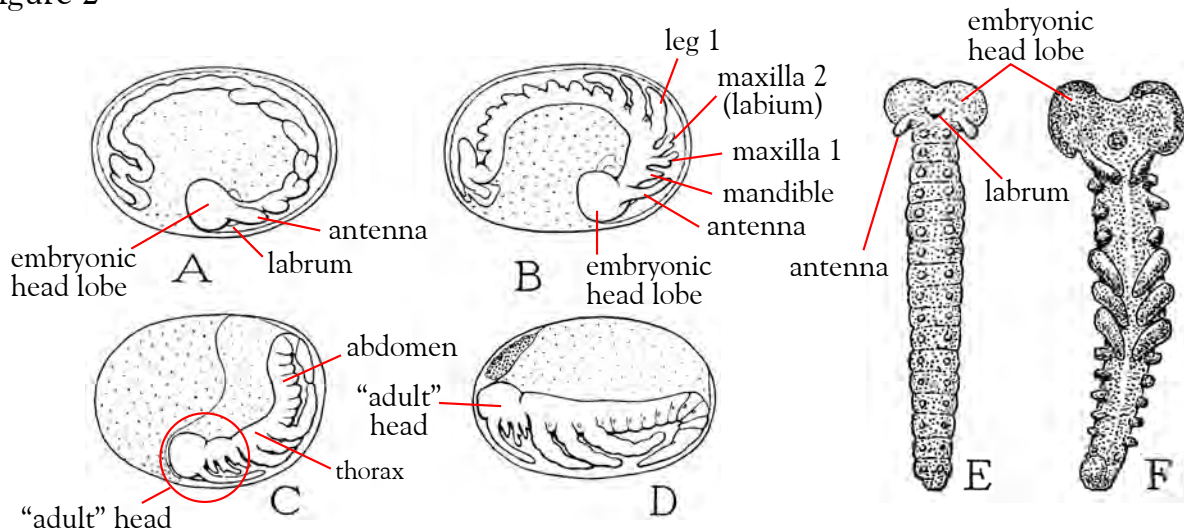


Well, the insect occurs in an adult stage and a larval stage ... or a juvenile stage ... and if we look to the adult for facts about the segmentation of the head, it won't tell us anything at all, because whatever segments are ... there are in the head are so condensed that you can't tell where the lines of separation may have been. And, so, we're reduced to the larva... or the embryo, rather ... for what facts we can get at. Then ... then again, some people will claim that the embryo itself is not reliable. The embryo is said to repeat its life history ... or its ... not its life history but its race history [2]. But it can't do that. The embryo, being shut up in an egg shell, it can't develop in the same way that its free-living ancestors evolved, so we have to interpret the embryo more or less. And so some people have discarded the embryo ... embryonic evidence and fall back on theories. And so some of their ideas are purely theoretical, but I am going to try to get at some of the facts.

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Figure 2



A-D, Four stages in the development of an earwig inside the egg, lateral view.

E, Diagrammatic ventral view of early insect embryo. F, Ventral view of mantis embryo at a later stage in development.

Now the insect embryo in its typical form has a large, usually bilobed head at the anterior end and then a long body stretched out on the underside of the egg. Then the mouth where the ... The mouth is the place where the stomodaeum grows in. And it's usually back at the rear end of the head lobe and following this are the segments. Now that would be the start of the embryo, but very soon, it ...

Can you see is that? Is that bright enough ... heavy enough to see?

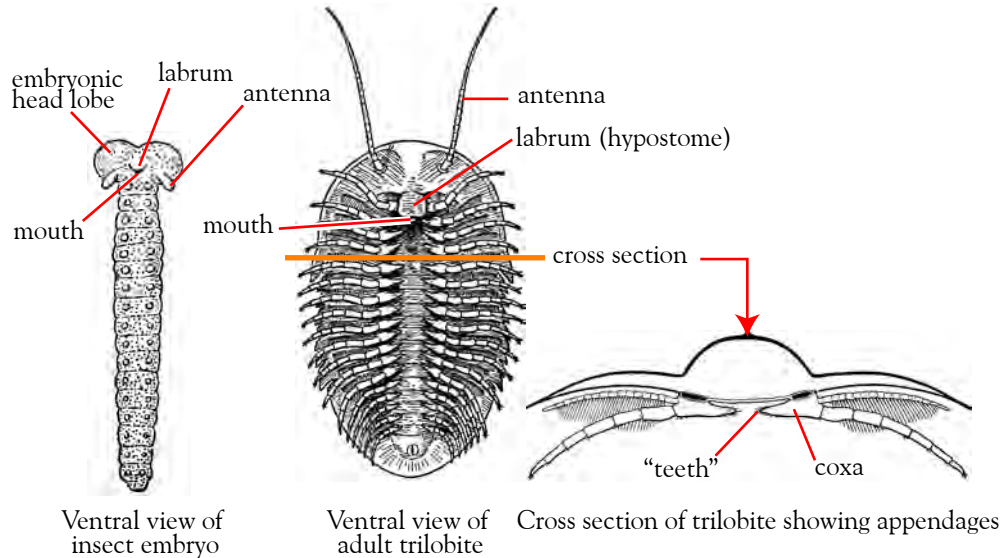
Pretty soon, of course, it takes on another form in its evolution ... There would be about 19 of these [segments] all together, but I lost count. The next thing is that the rudiments of the appendages grow out. Then, on this head lobe would be a pair ... there would be the antennae. The eyes would be formed from there. Then on these segments would be a pair of small lobes. Well, that's how, the ... Then, in front of the mouth, there's this big lobe called the labrum. Now, that would be a very primitive stage, I think, in the evolution of the insect, because in the next stage those appendages, some of them get larger. The next stage, then, there's an appendage -- these are the segments behind the head -- become larger and you can see that the ... what they're going to be. These lobes you see in pairs down here will, of course, be the legs, and these pairs ... these three pairs up here would be the mandibles, first maxillae and the second maxillae, but those on the abdomen have disappeared.

Now, here's a couple of words that ought to be distinguished. You see, you can call these lobes here that are going to be something, you can call those rudiments. But the others that disappeared ... that don't become anything ... you assume that they have been something in the past. You could say that this represents a "disappearing-centipede" stage in the evolution of the insects when presumably all these things were legs. But those that are ... have been reduced and never become anything more than pairs of lobes and then vanish, they're properly called vestiges. Now, those two words are often ... Rudiment in Latin means "preliminary sketch for a picture" or "a statue roughly cut out, unfinished." Well, so, anything that is going to grow into something else, something mature, can be called a rudiment, but those that have degenerated (gone backward in their growth) are properly called vestigial. That comes from *vestigium* in Latin. [It] means "a footpath", something that has been but is gone. Well, the two words are often mixed up. We often see descriptions of ... in the works of others that ought to know better saying that something, some organ or part, has been reduced to a rudiment. Now, that's incorrect usage of the word entirely. Because, as I say, the rudiment is something that has a future and a vestige is something that has a past.

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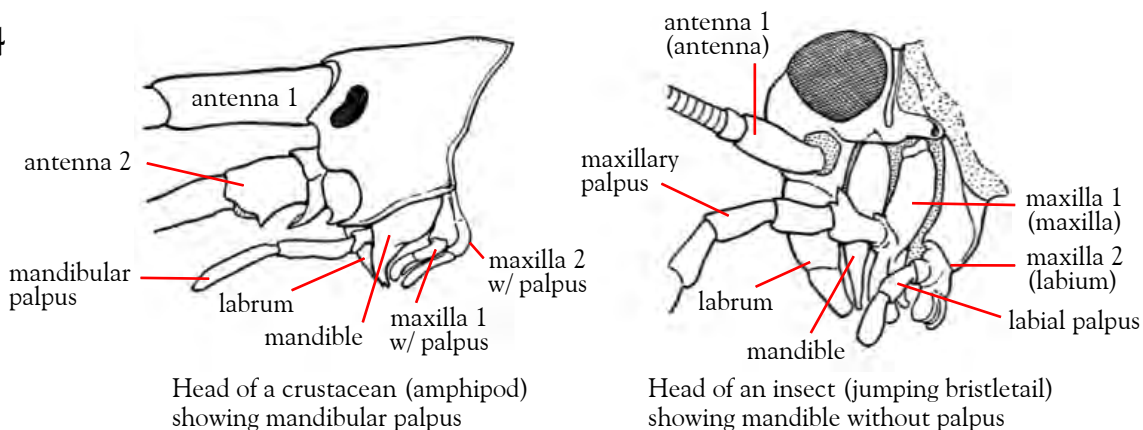
Figure 3



Well, when we get the insect down to this stage here ... Then it doesn't have a head anything like the adult. It's got that embryonic head lobe and just a series of appendages. We know -- I feel very sure, at least -- that in the evolution of the arthropods or the insects that all these appendages beginning with the mandibles on back were once legs. So, at this stage the insect has no head at all except that primary embryonic head lobe. And I don't suppose that the original insects had such a large head as that either because probably ... because the ... I mean the principal sense organs are in that lobe and it gets a precocious start. Just the same as a vertebrate embryo head is disproportionately large. But, that's all the head that the insect ... the arthropods had to begin with, undoubtedly, because that shows up in the embryos of all of them.

So ... But behind that they had a series of legs. That's shown in the trilobites, for example. They have a whole series of legs, but nothing else but legs behind the mouth. And the trilobite leg is a ... There's a coxa ... like that ... and then a long shaft ... with segments. But this coxa has teeth on the inner end of it and the other ones ... [?] ... So, it is supposed, and probably rightly, that the trilobites used those teeth on the ends of their coxae, you see, to grasp their food, whatever it may have been, pass it up toward the mouth. In front of the mouth, they did have a labrum [3], like this. So, you can imagine the mouth was in here. The labrum would be in there. The labrum was a lobe that sort of stopped the food as it was passed forward. You see a whole series of these legs; all worked together and passed the food up. Catch it anywhere and pass it on to the mouth. At least, that's what is supposed, and that's the only thing you can deduce from the structure.

Figure 4

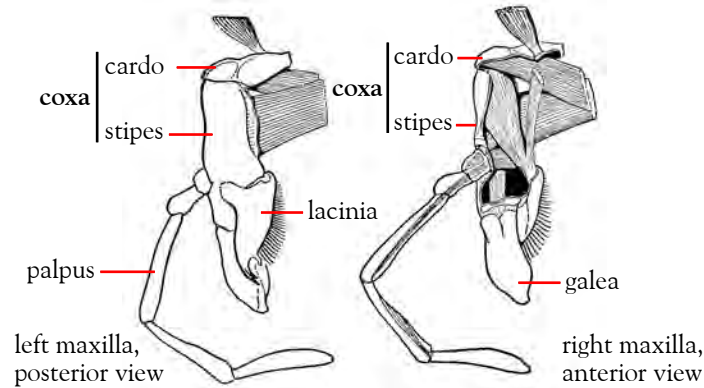


But it's very easy to see now that the mouthparts are derived from legs. Take the mandible, for example. It's represented roughly by a thing like that. It wouldn't suggest in itself a leg, but if you look at the mandible of some of the crustaceans. It has a little segmented palpus growing out on the side, and so you see that's just a rudimentary ... a

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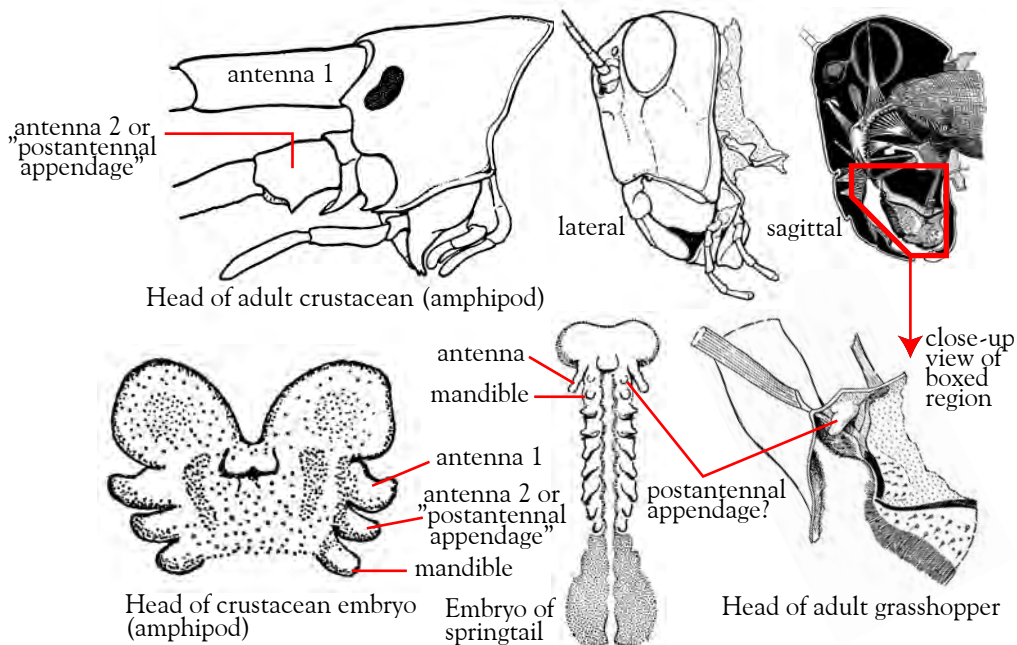
Figure 5



Maxillae of a cockroach, *Periplaneta americana*

Well, the same is probably true of the maxillae ... See there's the palpus, again ... segmented part of the appendage ... might well be remnants of a leg. Now, some people think that the cardo -- the cardo and this part we call the stipes -- are two segments of an appendage. But you can see how they are attached on the head. You see that the opening into the head goes all along there, so it's both of them. And there are no muscles between the cardo and the stipes. So, I should say that, again, both cardo and stipes, you see, are the coxa. And that joint between the cardo and stipes is simply for mechanical purposes and allowing the maxilla to work back and forth. See what I am talking about right here on the head ... that part? Why, the muscles can come in here ... and straightens out by pushing the thing out like that. So, that's just an adaptation for making that basal part moveable, or making the whole appendage moveable by stretching and bending that basal segment, which only should be called a coxa.

Figure 6

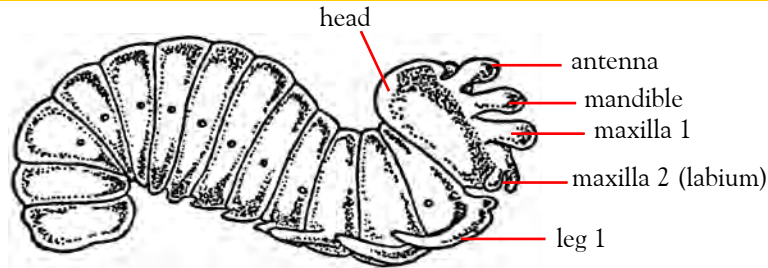


Well, as I say, there's evidence, any way you want to look at it, that the primitive insect had simply this head lobe and a series of legs. But the first ... the first of these sometimes has little vestiges of appendages on this first segment here which never develop into anything in the insect. But if we look at the embryo of a crustacean, you can see that [it] develops a pair of appendages, and those are what become the second [antennae]... These would be the first antennae of the crustacean (what the carcinologists call the antennules) and that segment there would be the segment that ... that forms the second antennae of the crustaceans, which are well-developed appendages. So, those little vestiges in there probably represent the second antennae of the crustacean, and possibly the insects had something there... in there, we don't know.

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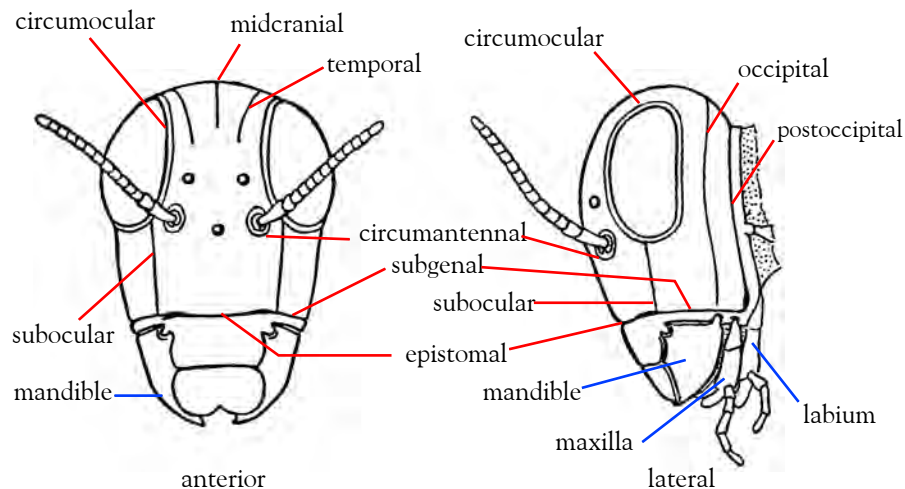
Figure 7



Embryonic caterpillar of the cabbage butterfly, *Pieris rapae*

Now ... now, you see, to give us a modern head, these segments have to be somehow combined with the embryonic head, and that's what actually happens. Here's a young caterpillar I drew, taken from ... [?] This curved over like that.... and had a big head lobe... and a segment in here... I'm drawing this very roughly to save time. Then there are three leg rudiments there. That would be a section of the embryo. This would be the head ... This would be the mandible ... first maxilla ... the second maxilla and these are the legs and those are the vestiges. But as the embryo grows the head looks like this ... [?] Now, let's take the picture published by a man who worked out the -- Eastham is his name -- worked out the embryology of the cabbage butterfly [5]. And it shows actually how all of those parts unite to form the head of the caterpillar. But this condition, of course, is very primitive yet. But, it demonstrates the fact, then, that there are four segments added to the embryonic head lobe. So, that's one thing we can be sure of in the matter of counting segments in the insect head, that there are four postoral segments that become a part of the definitive head. I'll show you later that there's a discussion, much discussion, about whether this head lobe itself is formed from segments, but that will be theoretical. And, so, the one thing that we can ... we can be sure of is that there are these four segments added to the head lobe.

Figure 8



Generalized head of an orthopteroid insect showing major sulci (or "sutures")

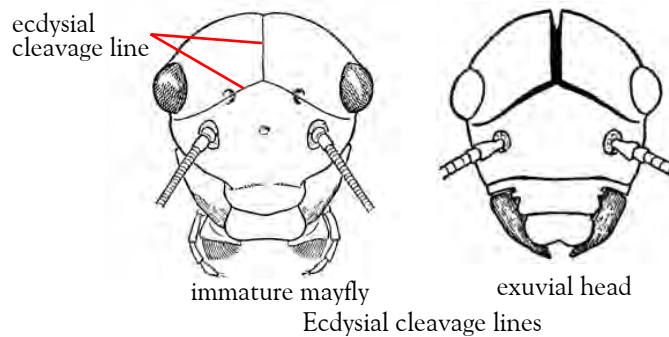
So, if we look at a head of an orthopteroid insect ... Right in there.... Now the mandibleyou see is quite...???.. head.....Then comes the ... right directly behind it is the maxilla ...???... but then a groove that runs up ... down near the rear end... the margin of the head and the labium is always suspended from ... from that. Well ...???... the embryo has three separate sets of appendages, and we can assume that the segments are combined in that adult head. But, you see, there are no lines in this case there to show you where the limits of the segments, except that there is that groove toward the ... near the rear margin of the head that... and the flange behind it carries the labium. It looks reasonable to suppose that's ... There's the labial segment. And this may be a division between the mandibular segment and the maxillary segment. I was going to say that is more or less just based on appearances ... But the ... no lines mark the limits of the other segments at all, although you'll find in some of the other discussions, the various grooves are ... have been identified ... or not identified, but interpreted as intersegmental lines. But, as a matter of fact, the ... these lines are simply grooves that form internal ridges for strengthening the skeleton of the head or for giving attachment to muscles. And they're what you've always called sutures and have no relation whatever to the primitive segments of the head. So, I think that idea is about gone. Although it has been worked up in some detail in the past by students of head segmentation, so called.

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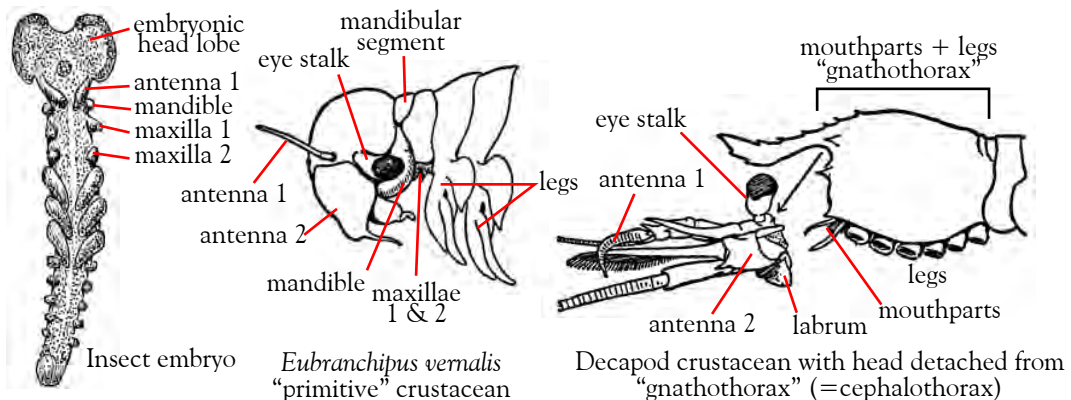
And another thing, as I say, these lines called sutures, are really not sutures at all, because a suture properly is a place where two things are grown together. It comes from a Latin word meaning "a seam." So, I don't know for example ... you often <Snodgrass draws sutures>another one... another one like that... Well, as I say, most of those are separate grooves in the skeleton, but very clearly are for mechanical purposes, and they have nothing to do with the original segmentation and, also I've said, the term suture is improperly applied to them, because a suture means a line along which things have grown together. And, undoubtedly, the early entomologists were acquainted with the vertebrate skull -- human skull, for example -- where bones are grown together along lines -- those zigzag margins -- that look like they've been sewed together and that gave them the idea of calling those things sutures. Which they really are things that have grown together. But, knowing that, then, they look at the insect and wherever these lines on the insect head are ... the natural thing is to call them sutures. So they did, and the suture term has come down to us ever since. But I said it is much better to call them grooves or give them the Latin word *sulcus* ... s-u-l-c-u-s. Sulcus means a groove or furrow. Sulci ... s-u-l-c-i ... would be the plural of it. So, in all my recent writings, I've changed the names of these grooves in the head to sulci instead of sutures.

Figure 9



But one principal one in here that sometimes I called... has been called the epicranial sutures that is undoubtedly not the ... is simply the line where the skin is split. Where the insect comes out of its old skin... It's an ecdysial line. That word "epicranial suture" has become quite a standard part of the nomenclature of the insect head. But some years ago, I wrote a paper to show that is not a suture at all, [but] simply a line where the cuticle splits in ecdysis. And I think that idea is... I think I got that idea across [6].

Figure 10



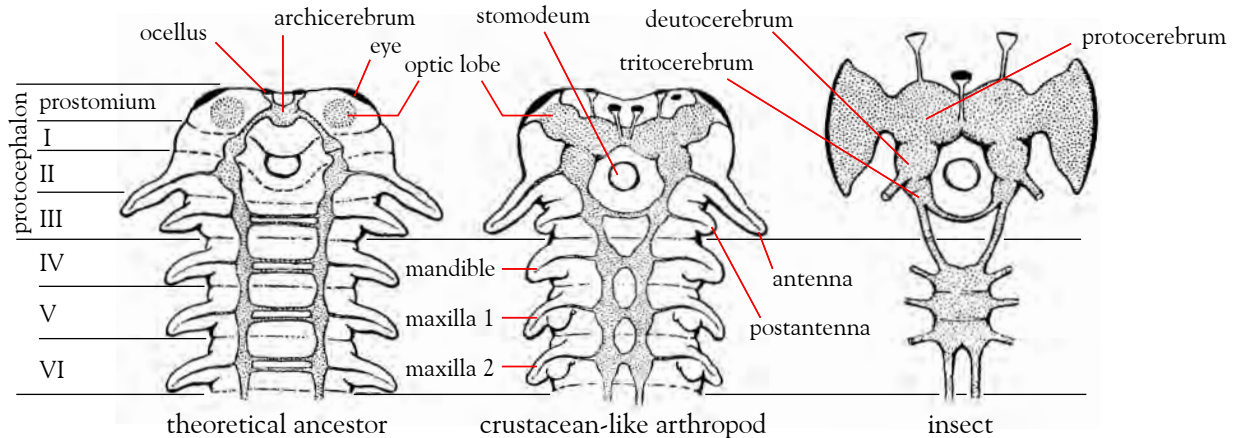
One mustn't think that ... that all the arthropods have a head of this kind, because they don't. Well, if you look at this stage here ... and most of them have appendages... I mean flexible appendages all along the body ... but these segments don't always combined with the head ... Although, for example, there's a ... small crustacean ... primitive crustacean ... has a head like this... The eye, as in many crustaceans, comes out here on a stalk. Well, this up here that's all see that corresponds, I think, with the ... with this head there, except that this thing down here is the second antenna. Then behind this... behind this cute little segment, wedged in here ... it carries the mandible... right like that ... and another segment that carries two little remnants of the maxillae. Well, you see there's a case where the adult head has not absorbed the gnathal segments, although it has taken over the second antennae ... these. But the mandibular segment is a distinct segment behind it and that is true also of a lot of the higher crustaceans, the decapods, for example. You can take off this little head piece underneath the front spine of the carapace ... it can be easily detached ... and it has exactly that same structure. As I say, it carries the eyes, the labrum is here ...???... and the antennae... So that ... the head can be formed just from that part

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there ... what becomes of that segment the appendages themselves are not taken into the adult head ...???... And then a crayfish would look like this... that would be the carapace, and down in here would be the head lobe and here's the two pairs of appendages and antennae and ... and the mouth and can be easily separated from the rest of the animal. And that is undoubtedly the same thing as this. And it is the head, because it contains the brain, supports the eyes. The eye stalks usually stick out here like that. So, there's no rule, you see, at all about the formation of this head in the... in the arthropods. And yet the carcinologists continue to regard the head of a crayfish, or a lobster, a crab as including these gnathal segments, which they don't at all. They're all combined with thorax under that carapace. And while they call that whole business the cephalothorax, why it's better to call it the gnathothorax, meaning that's a combination of the gnathal segments and the thoracic segments. But it's hard to convince the carcinologists of that because they've used their terms for so long. Most taxonomists are very reluctant to change their names, but that's how it is.

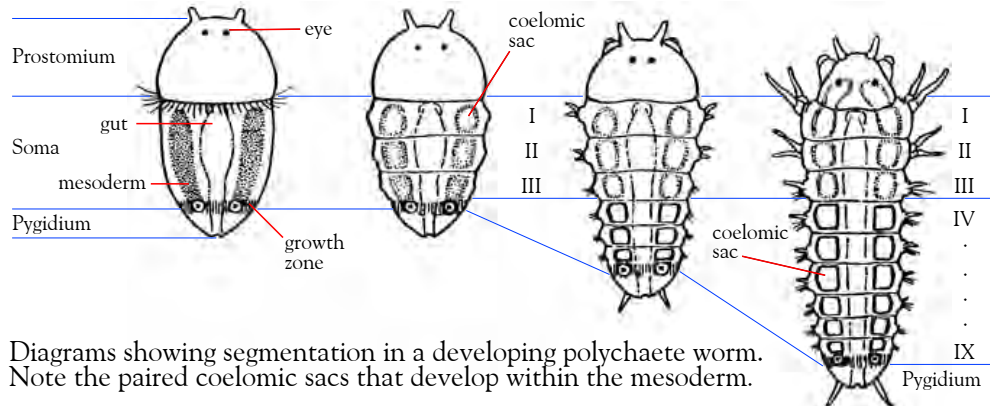
Figure 11



One of many views on the segmental composition of the nervous system of the insect protocephalon, the hypothetical ancestral "head" that corresponds to the embryonic head lobe or blastocephalon.

Well, you see, then, we do have some facts here from the embryo which shows you that the adult head contains at least four segments that were originally body segments. But in all the textbooks and papers on the head, you still read that the insect head consists of six segments. Well, maybe it does. But that implies, you see, that there are two ... at least two segments in that embryonic head. Well, the other idea was that it ... You see it contains the brain and part of the brain innervates the eyes. The next part of the brain gives off the nerves to the antennae. And those two sense organs belong to this embryonic head lobe. "Embryonic head lobe" is an awkward term, maybe. DuPorte [7] in Canada has invented the term *blastocephalon* for it. The word *blasto-* doesn't mean "blast", it means "a sprout" or "something growing" and has been commonly used, you see, by the embryologists to mean some part of the embryo. So, we have blastoderm and blastocoel and blastopore and a lot of other things. Just means part of the embryo. Blastocephalon, then, means the embryonic head. Now, that's a good term, because it doesn't imply that it's a primitive head at all. It might be, but it makes no such implication.

Figure 12



Diagrams showing segmentation in a developing polychaete worm. Note the paired coelomic sacs that develop within the mesoderm.

Well, in later times, and [I've] written at times, the of the head has been ... segmentation of the head has been based on study of the mesoderm. Well, it is found that in the head lobe there are two pairs of little cavities in the mesoderm which are regarded as coelomic sacs. And so, that has given us a second basis for the belief that the embryonic head lobe contains ... is a segmented area or, at least, that it was primarily segmented. But the

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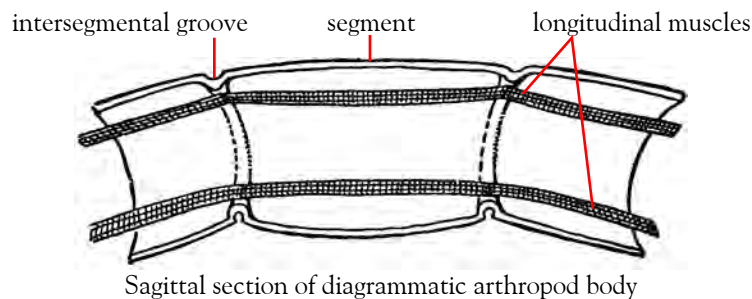
coelomic sacs correspond with the antennae ... the first ... the second pair with the antenna ... the first pair, however, evolved between the ... the eye part of the brain and the antennal lobe and have been called preantennal coelomic sacs. So we have in the head, a pair of preantennal coelomic sacs and a pair of antennal coelomic sacs. So, then, it is by ... according to this idea that those coelomic sacs represent segments, which I'll discuss presently. The head would be composed of... I mean, the embryonic head would be composed of two segments and a prostomium... or a primary anterior part ... called a prostomium in the worms, which includes the eyes and the eye part of the brain and the labrum. Well, the embryologists place a great deal of importance on these coelomic sacs as indicators of segmentation. And it is true that you can take a part of the body of the early embryo that isn't yet segmented and the mesoderm forms two bands along the sides like this, but it later becomes divided into solid blocks. There are solid blocks at first ... This is not found [so much?] in the insects, but in the Onychophora, some of the lower crustaceans, worms, that's what happens to the mesoderm. And then the mesoderm blocks become hollowed out, like that. As I say, most of the embryologists have such faith in these coelomic sacs occurring like that -- a series inside the body -- that they call the formation of these sacs themselves segmentation ... call those coelomic sacs the somites. Well, that doesn't seem reasonable to me, because at first ... no segmentation of the body ...

BELL

Is it quittin' time?

Bickley: Whenever you get to a good stopping point.

Figure 13



Sagittal section of diagrammatic arthropod body
Segmentation as defined by Snodgrass; formation of external grooves by attachment of longitudinal muscles to form skeletomuscular "motor units"

Snodgrass: Well, I was going to say, what happens here is that the outer walls of these sacs form ... form the muscles... Suppose these muscle have been formed by those cells. The attachment ... attachment of muscles makes the body wall, you see. Come in, and grooves, right there, is what I would call a true segmentation of the animal after the muscles have come and divided the body in to these motor units.

Well, your ideas from then on will differ according to your definition of a segment. Likely you all know ... some of you entomologists studying the adult animal ... realize that the segment is the subdivision of the body by the muscle attachments into a succession of motor units. Well, that's the point that I would regard as true segmentation rather than simply the formation of these coelomic sacs, because, as I say, of course, the coelomic sacs mostly go to pieces later on.

Well, next time, then, I'll have to finish up on this subject. But some of what I said today will be very good material for discussing the possible evolution of the arthropods from some primitive form like this.

Well, that's ... all I have to say.

APPLAUSE

Well, I hope that my lecture was as good as your applause.

Bickley: We'll have time for questions next time.

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NOTES

1. Snodgrass used the terms “facts” and “theories” to separate empirical observations from the evolutionary and phylogenetic speculations drawn from these observations. His use of the term “theory” does not correspond to the modern concept of hypothesis. To Snodgrass, theories were evaluated by their relative plausibility and thereby always retained an element of subjectivity and uncertainty. This fact-theory dichotomy probably reflects Snodgrass's intellectual development in the late 19th and early 20th century, when comparative biology was often equated with “natural history” and seemed incapable of offering explanations of biological phenomena as rigorous as those provided by emerging experimental disciplines (see Bowler, 1983, 1996). Working without generally accepted methods of evolutionary and phylogenetic analysis, Snodgrass chose to focus on the facts and only toyed with theories. As a consequence, Snodgrass' reputation for producing high quality empirical work has persisted, while the reputations of those who promoted “theories” have tended to rise and fall with the theories themselves.

Bowler, P.J. 1983. *The Eclipse of Darwinism*. Johns Hopkins University Press, Baltimore.

Bowler, P.J. 1996. *Life's Splendid Drama*. University of Chicago Press, Chicago.

2. Snodgrass is referring here to 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 thought that embryos recapitulated evolution in a significant way. Perhaps because development can be observed and described as rigorously as anatomy, 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.

3. This structure is termed the hypostome by trilobite workers and is assumed to be homologous, at least in part, to the labrum of other arthropods. For additional information on trilobite anatomy, go to the web site *A Guide to the Orders of Trilobites* by Sam Gon III (<http://www.trilobites.info/index.htm>)

4. The coxa or gnathobase model for the origin of insect mandibles was eclipsed for nearly four decades by S.M. Manton's (1964, 1977) hypothesis that the mandible represents an entire appendage, not just the coxa. However, Manton's proposal was never universally accepted by arthropod morphologists, and both morphological (Weygoldt 1986; Kukalova-Peck, 1992) and developmental (Popadic *et al.*, 1998) evidence have convinced most that the gnathobase model promoted by Snodgrass is correct.

Kukalova-Peck, J. 1992. The “Uniramia” do not exist: the ground plan of Pterygota as revealed by Permian Diaphanoptera from Russia (Insecta: Paleodictyopteroidea). *Canadian Journal of Zoology*, 70: 236-255.

Manton, S.M. 1964. Mandibular mechanisms and the evolution of arthropods. *Transactions of the Royal Society of London, Series B*, 247: 1-183.

Manton, S.M. 1977. *The Arthropoda: Habits, Functional Morphology, and Evolution*. Clarendon Press, Oxford.

Popadic, A., G. Panganiban, D. Rusch, W.A. Shear & T.C. Kaufman. 1998. Molecular evidence for the gnathobasic derivation of arthropod mandibles and for the appendicular origin of the labrum and other structures. *Development, Genes & Evolution*, 208: 142-150.

Weygoldt, P. 1986. Arthropod interrelationships - the phylogenetic-systematic approach. *Zeitschrift fuer zoologische Systematik und Evolutionsforschung*, 24: 19-35.

5. Eastham, L.E.S. 1930. The embryology of *Pieris rapae* - organogeny. *Philosophical Transactions of the Royal Society of London, Series B*, 219: 1-50.

6. Snodgrass, R.E. 1947. The insect cranium and the “epicranial suture”. *Smithsonian Miscellaneous Collections*, 107(7): 1-52.

7. DuPorte, E.M. 1953. The protocephalon: a critique of recent interpretations. *Canadian Entomology*, 85: 41-55.

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Figure Credits

Figure 1. Snodgrass, R.E. 1960. Facts and theories concerning the insect head. *Smithsonian Miscellaneous Collections* 142(1): 1-61, figs 1, 3.

Figure 2. A-D, Snodgrass, R.E. 1928. Morphology of the insect head and its appendages. *Smithsonian Miscellaneous Collections*, 81(3): 1-158, fig. 16. E, F. Snodgrass, R.E. 1960. Facts and theories concerning the insect head. *Smithsonian Miscellaneous Collections*, 142(1): 1-61, fig. 1A, B.

Figure 3. Insect embryo: Snodgrass, R.E. 1960. Facts and theories concerning the insect head. *Smithsonian Miscellaneous Collections*, 142(1): 1-61, fig. 1A. Trilobite, ventral view: Snodgrass, R.E. 1958. Evolution of arthropod mechanisms. *Smithsonian Miscellaneous Collections*, 138 (2): 1-77. fig. 16A. Trilobite cross section: Snodgrass, R.E. 1935. *Principles of Insect Morphology*. MacGraw-Hill Book Co., New York, fig. 45.

Figure 4. Snodgrass, R.E. 1951. *Comparative Studies of the Head of Mandibulate Arthropods*. Comstock Publishing Co., Ithaca, NY. figs 19E, 32A.

Figure 5. Snodgrass, R.E. 1935. *Principles of Insect Morphology*. MacGraw-Hill Book Co., New York, fig. 80.

Figure 6. Amphipod adult: Snodgrass, R.E. 1951. *Comparative Studies of the Head of Mandibulate Arthropods*. Comstock Publishing Co., Ithaca, NY, fig. 19E. Amphipod embryo: Snodgrass, R.E. 1960. Facts and theories concerning the insect head. *Smithsonian Miscellaneous Collections*, 142(1): 1-61, fig. 1F. Embryo of springtail: Snodgrass, R.E. 1928. Morphology of the insect head and its appendages. *Smithsonian Miscellaneous Collections*, 81(3): 1-158, figs 22D. External view of grasshopper head: *Ibid.*, fig. 36A. Internal view of grasshopper head: *Ibid.*, fig. 41. Close up view of grasshopper head: *Ibid.*, fig. 42B.

Figure 7. Snodgrass, R.E. 1958. Evolution of arthropod mechanisms. *Smithsonian Miscellaneous Collections*, 138 (2): 1-77, fig. 15E.

Figure 8. Snodgrass, R.E. 1960. Facts and theories concerning the insect head. *Smithsonian Miscellaneous Collections*, 142(1): 1-61, fig. 6A, B.

Figure 9. Snodgrass, R.E. 1960. Facts and theories concerning the insect head. *Smithsonian Miscellaneous Collections*, 142(1): 1-61, figs 7A, 8B.

Figure 10. Insect embryo, *Eubranchipus*: Snodgrass, R.E. 1960. Facts and theories concerning the insect head. *Smithsonian Miscellaneous Collections*, 142(1): 1-61. figs 1B, 2C. Decapod: Snodgrass, R.E. 1958. Evolution of arthropod mechanisms. *Smithsonian Miscellaneous Collections*, 138 (2): 1-77, fig. 15I.

Figure 11. Snodgrass, R.E. 1928. Morphology of the insect head and its appendages. *Smithsonian Miscellaneous Collections*, 81(3): 1-158, fig. 15.

Figure 12. Snodgrass, R.E. 1938. Evolution of the Annelida, Onychophora, and Arthropoda. *Smithsonian Miscellaneous Collections*, 97(6):1-159, fig. 11.

Figure 13. Snodgrass, R.E. 1935. *Principles of Insect Morphology*. MacGraw-Hill Book Co.: New York, fig. 36A.