PHYSIOLOGY AND SYSTEMATICS

New genes are not produced but it is the way they are organized and the different developmental pathways they become involved in

“Interest in the links between development and evolution have been heightened recently by the discovery that developmentally interesting genes identified in one organism often have homologs (based on sequence similarity) in a range of distantly related creatures.” pg. 581 Patel

SYSTEMATICS AS PHYSIOLOGY

John Kennedy (famous insect behaviorist), in a chapter (see below) devoted to Sir V. B. Wigglesworth on his retirement) noted that behavior is the expression of an organism’s physiology

J.S. Kennedy. 1967. Behaviour as physiology, pp. 249-266. In: Insects and Physiology. Eds. J.W.L. Beament and J.E. Treherne. Oliver & Boyd, London.

The same should hold true for systematics.

Morphological traits, biochemical traits, etc., are the results of the organism’s physiology as orchestrated by the genetic system of the organism. Thus, Systematics as physiology is an appropriate topic for a course in Insect **Structure** and Function.

Think of it! Don’t most systematists use **structure** as a key to unlock the identity of a new species and to place it in its phylogenetic position.

INTEGUMENTRY SYSTEM

1. Identification using cuticular hydrocarbons or lipids

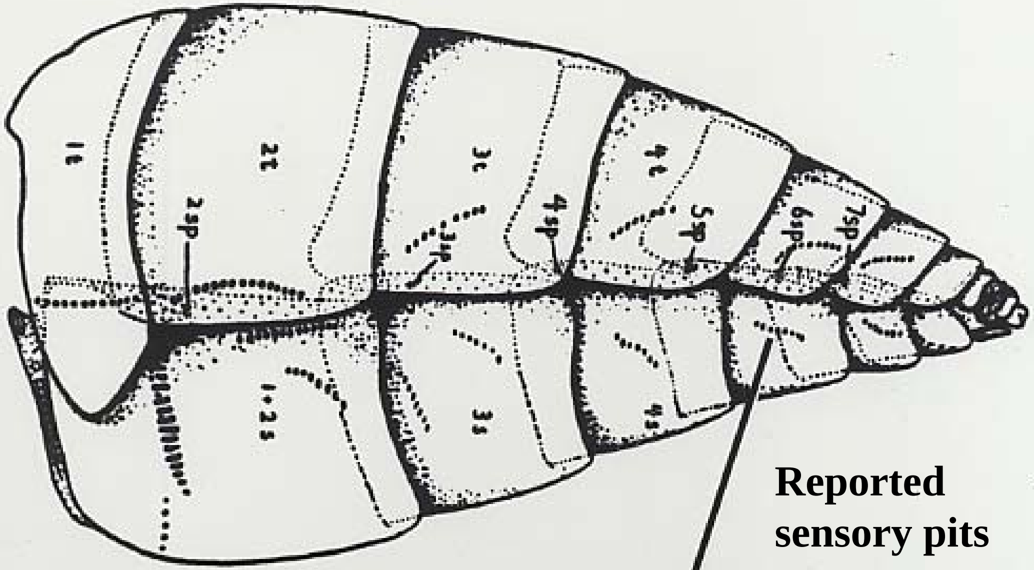
Neal, J.W., et al. 1994. Cuticular lipids of greenhouse whitefly and sweetpotato whitefly Type A and B (Homoptera: Aleyrodidae) pupal exuviae on the same host. Ann. Ent. Soc. Amer. 87:609-618.

2. Cuticular plaques and dipterous larval evolution

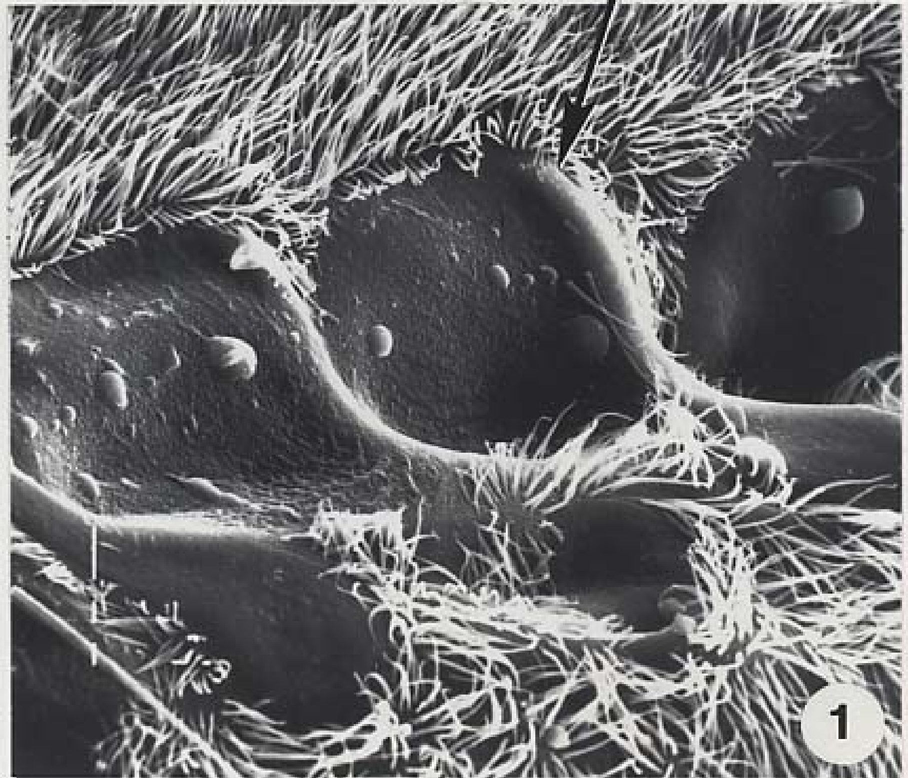
Stoffolano, J.G., Jr., N.E. Woodley and A. Borkent, and L.R.S Yin. 1988. Ultrastructural studies of the abdominal plaques of some Diptera. Ann. Entomol. Soc. Amer. 81: 503-510.

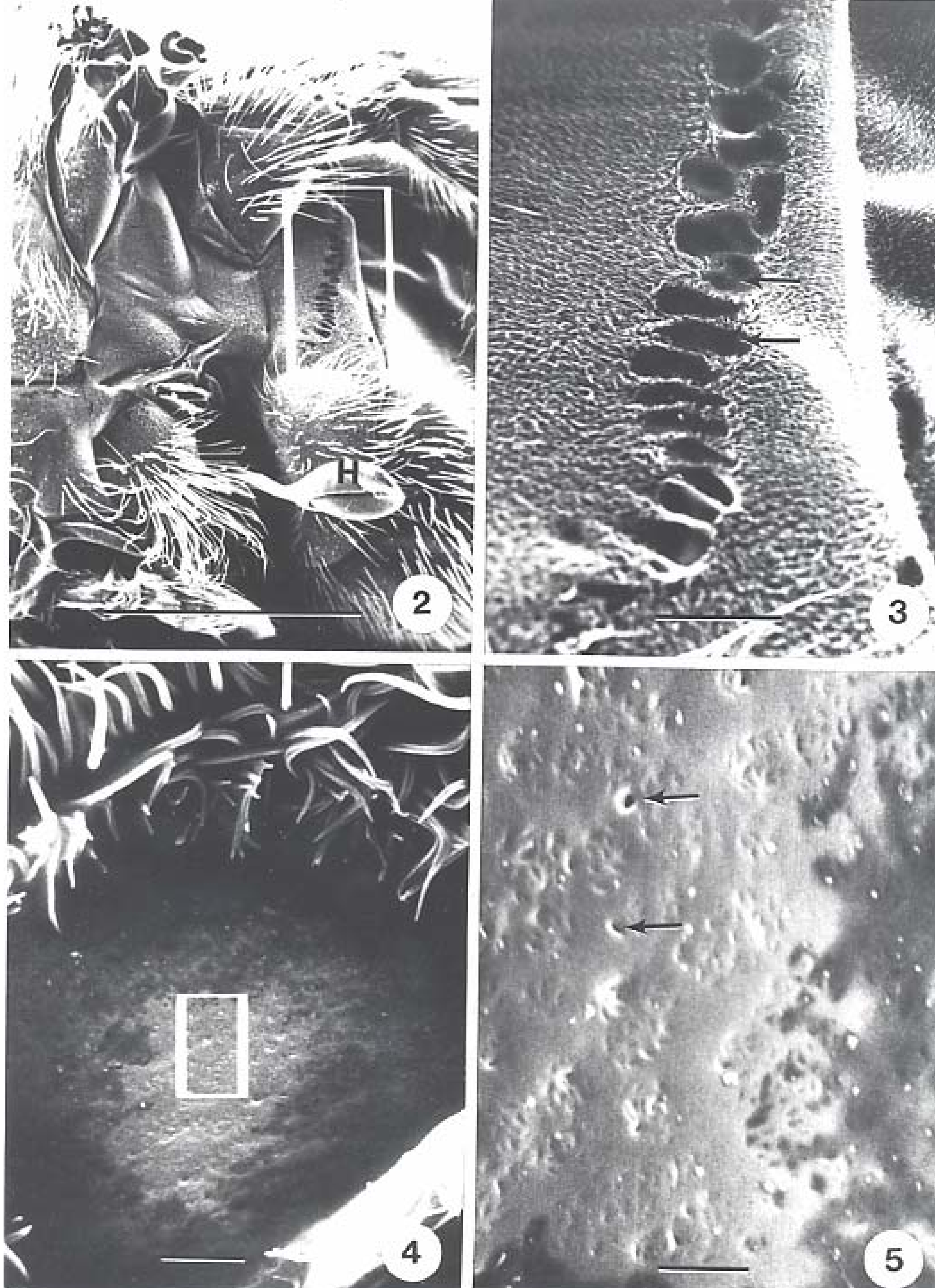
Yeates, D.K. and B. M. Wiegmann. 1999. Congruence and controversy: Toward a higher-level phylogeny of Diptera. Ann. Rev. Ent. 44: 397-428.

***Tabanus nigrovittatus* (above) feeding on blood or artificial diet containing ATP while below a female is taking a human blood meal. It was reported in the literature that the pits or plaques on the abdomen of the adult were sensory. Were they?**



Reported sensory pits





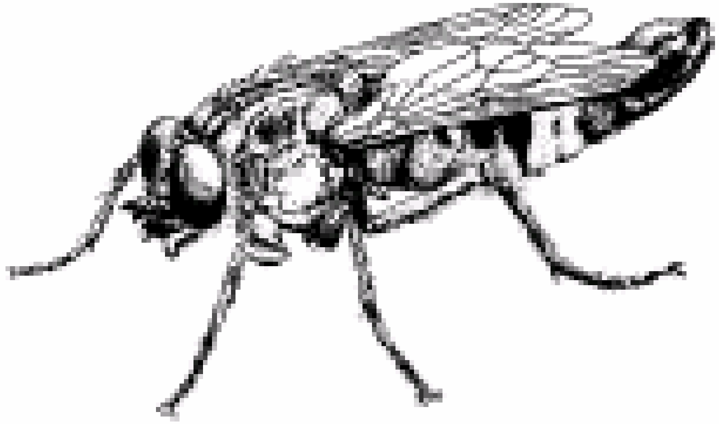
Different SEM magnifications of the supposed ‘sensory pits’ in female *Tabanus nigrovittatus*. Note in fig. 5 the pitting nature of the cuticle.

Stoffolano, J.G., Jr., N.E. Woodley and A. Borkent, and L.R.S Yin. 1988. Ultrastructural studies of the abdominal plaques of some Diptera. Ann. Entomol. Soc. Amer. 81: 503-510.

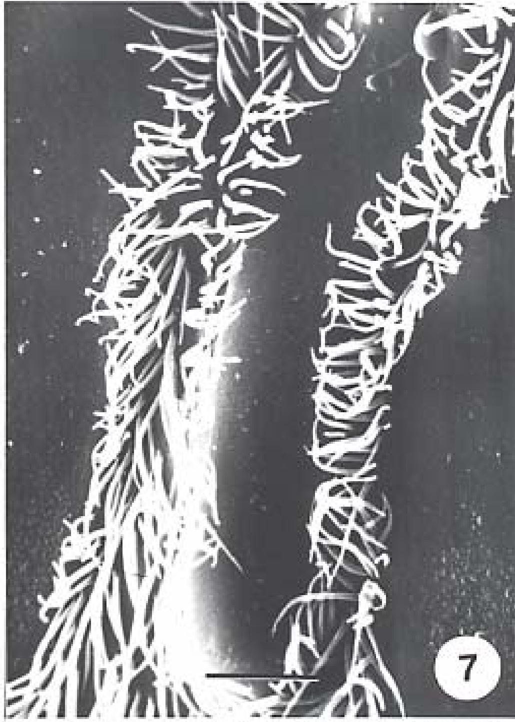
SEM of ventral view of male *Tabanus nigrovittatus* (figs. 6, 7) showing the pits. If they were involved in sensing temperature when the female lands on the host, why would they be present in the males?

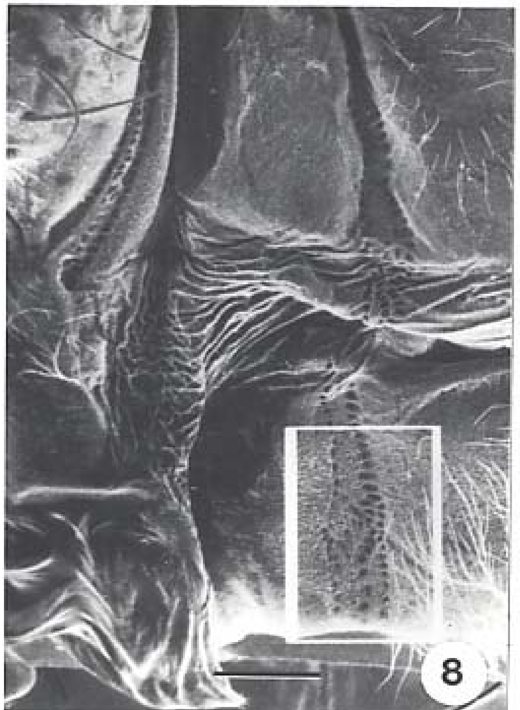
Apiocera barri (Cazier (Apioceridae) showing pits in fig. 8 with higher magnification in fig. 9.

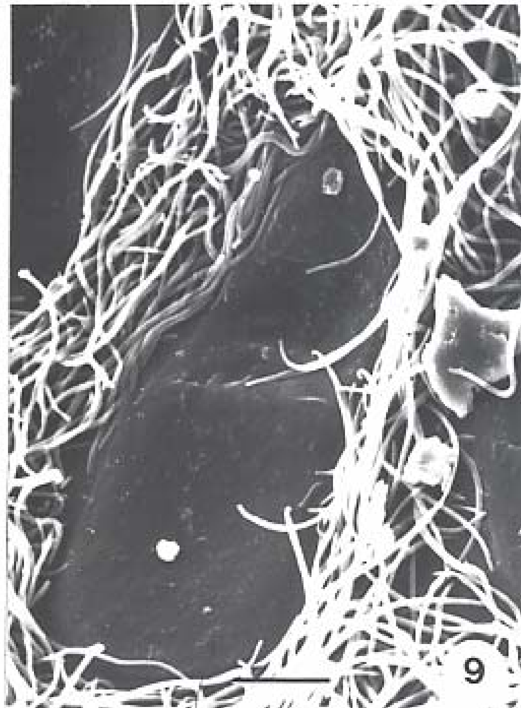
Flower loving flies




6


7

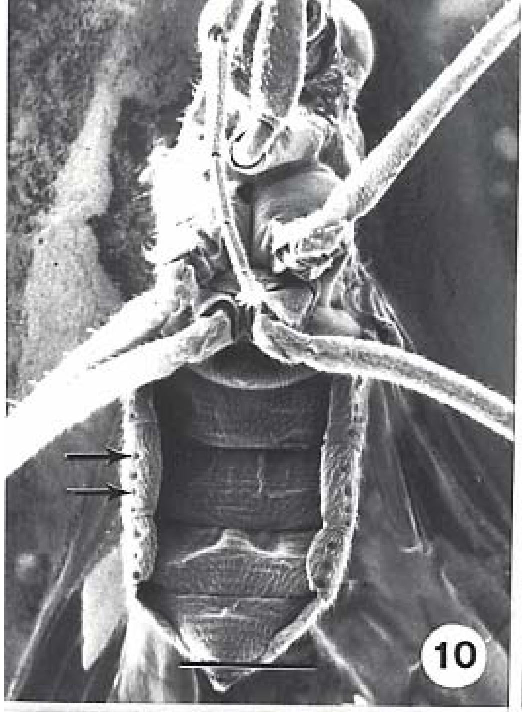

8

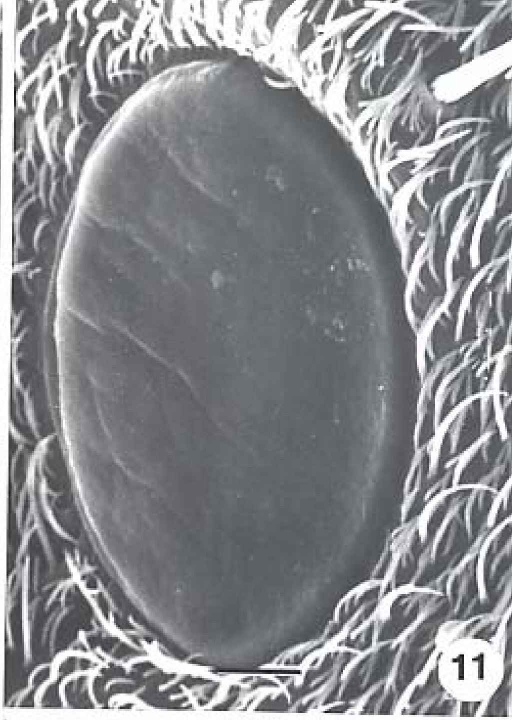

9

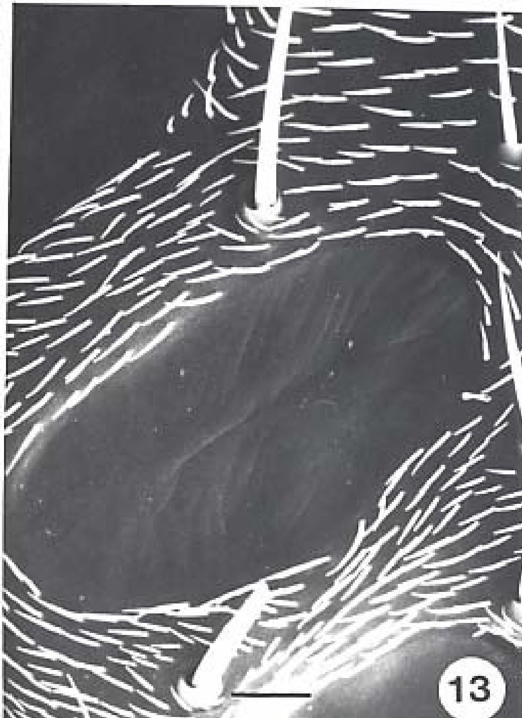
Hydrophorus viridiflos (Dolichopodidae) female showing pits on adult and their magnification.

Dolichopus consanguineas (Dolichopodidae) male showing the pits.

Long-legged flies

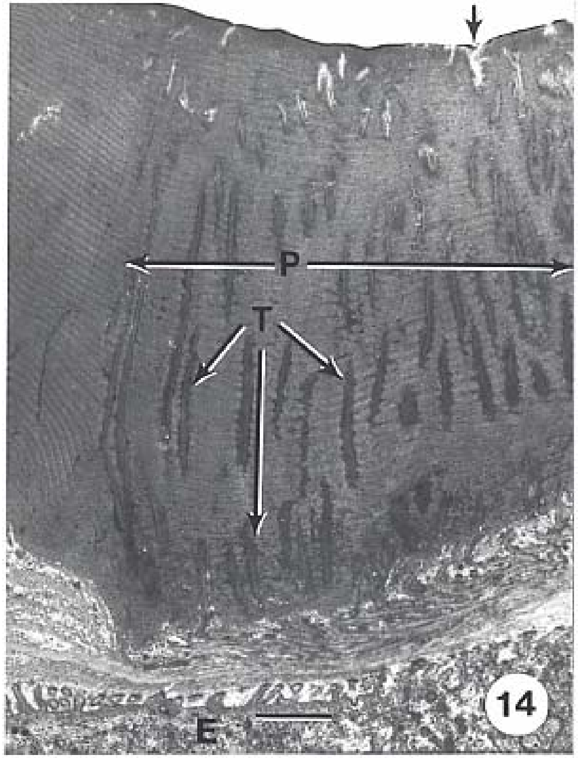


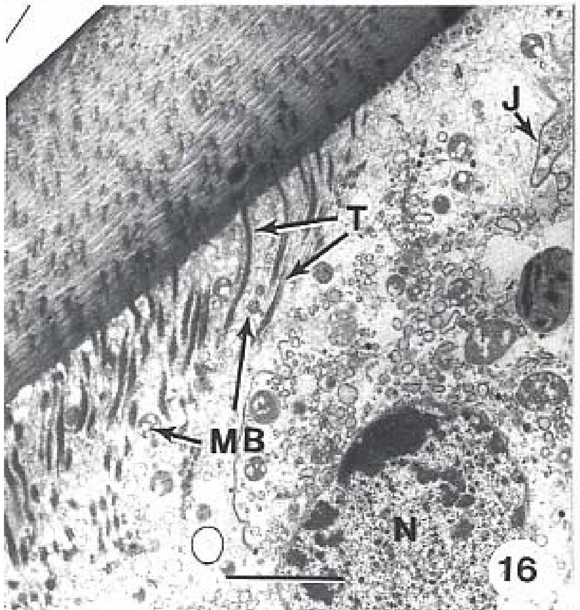


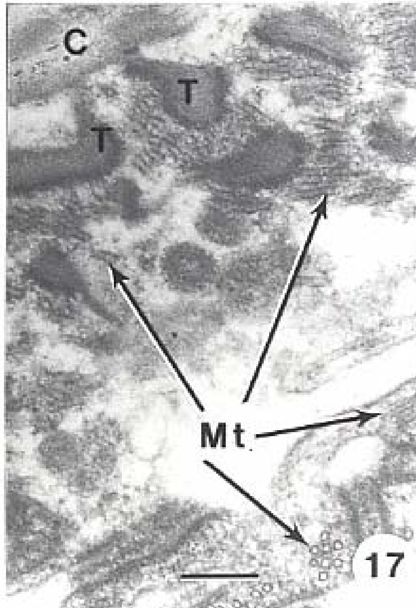


1. Literature said they were sensory pits
2. Hypothesis was they were heat detectors
3. Found in both sexes of hematophagous insects and that made us abandon the idea that they were heat detectors
4. Necessary to do TEM
5. TEM shows tonofibrillae in the cuticle and also in the specialized tendinous epidermal cells underneath, which could not produce a specialized cuticle since their function was for muscle attachment and tonofibrillar production
6. Worked with two systematists who provided other specimens and the idea of what they functioned as

Plaques only found in the nematocerous and orthorrhaphous brachycerous flies. Regions of muscle sets are used by the pupa for abdominal movements and for eclosion of the pharate adult. Once eclosion has taken place, the muscle sets degenerate. These pupae use these muscles to move from one area to another or deeper into the soil.







Gene expression's role in determining bristle patterns in flies

Usui, K, D. Pistillo and P. Simpson. 2004. Mutual exclusion of sensory bristles and tendons on the notum of Dipteran flies. Current Biology 14: 1047–1055.

Anyone who wants to successfully identify flies to family and beyond has to figure out and become comfortable with their chaetotaxy (patterns of bristles on the body). These bristle patterns are not random and show remarkable consistency on certain parts of the body, especially the dorsal surface of the thorax (the scutum of Diptera). Usui, Pistillo, and Simpson have discovered a link between the location of attachment sites for indirect flight muscles and the location of bristle rows on the scutum of flies. This is a great example of how internal morphology can influence external morphology. In addition, the authors go beyond the realm of classical morphology and provide experimental evidence linking the expression of several distinct genes and gene complexes to the development and segregation of tendon and bristle precursors. This evidence helps to explain what appears to be an evolutionary ground plan of four bristle rows on the scutum in Diptera.

Yeates, D.K. and B. M. Wiegmann. 1999. Congruence and controversy: Toward a higher-level phylogeny of Diptera. Ann. Rev. Ent. 44: 397-428.

Pg. 412. “Cyclorrhaphan monophyly is well supported with the following synapomorphies: (a) adult abdominal plaques lost (Stoffolano, J.G., Jr., N.E. Woodley and A. Borkent, and L.R.S Yin. 1988), (b) wing vein R4+5 unbranched, (c) pupa enclosed in a puparium formed by the hardened larval cuticle, (d) larva with cephalopharyngeal skeleton, etc.”

CHARACTER STATES

Maddison, D.R. 1994. Phylogenetic methods for inferring the evolutionary history and processes of change in discretely valued characters. Ann. Rev. Ent. 39: 267-292.

Reconstruction of character evolution or reconstruction of ancestral states

Is a reconstruction of how the trait changed in time and

Changes within the lineage

Character states mentioned or discussed in this unit

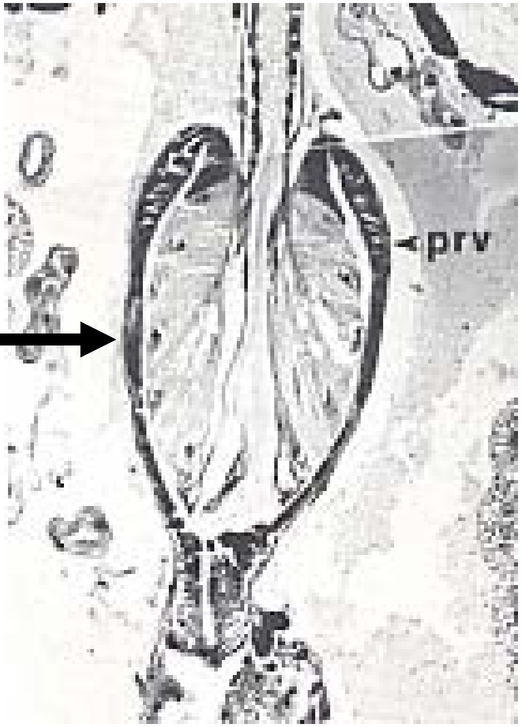
1. Digestive tract in Diptera
2. Germ band
3. Ventral nerve cord in Diptera

DIGESTIVE SYSTEM

King, D.G. 1991. The origin of an organ: phylogenetic analysis of evolutionary innovation in the digestive tract of flies (Insecta: Diptera). Evolution 45: 568-588.

Regular proventriculus

Cardia



OF ALL OF THE TOPICS (including systems) WE DISCUSSED THIS SEMESTER, WHAT TOPIC DO YOU THINK MIGHT HAVE THE GREATEST RELEVANCE TO SYSTEMATICS?

Genetic and molecular dissection of the mechanisms involved in development of the embryo. Are the mechanisms conserved, are they extremely different, and what are their evolutionary histories.

INSECT PRE-EMBRYONIC DEVELOPMENT

CHARACTER STATES

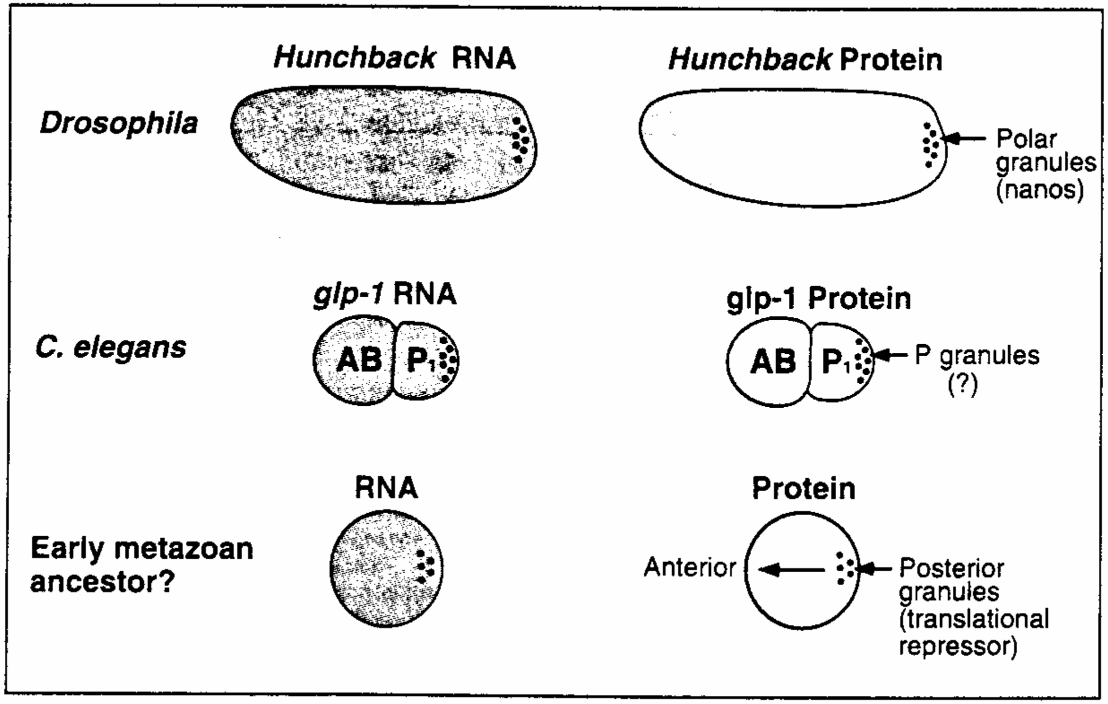
MECHANISTIC STATES OR PATHWAYS

Kimble, J. 1994. An ancient molecular mechanism for establishing embryonic polarity? Science 266 (28 Oct. 1994): 577-578.

"Worms, butterflies, and chimpanzees all have the same body axes- head and tail, front and back, and left and right sides."

"In both species (*Caenorhabditis* and *Drosophila*), translational repression at the posterior pole establishes asymmetry along the anterio-posterior axis. Nematodes and insects diverged at least 600 million years ago—when metazoans first made their appearance in the fossil record—and so such localized translational repression may be an ancient molecular mechanism for specification of one body axis, the anterior-posterior axis that runs from head to tail."

Similarity also exists in all 3 between the presence of posterior elements (polar bodies, P granules and 'germ plasm' in vegetal pole of *Xenopus* embryos) that will become germ cells.

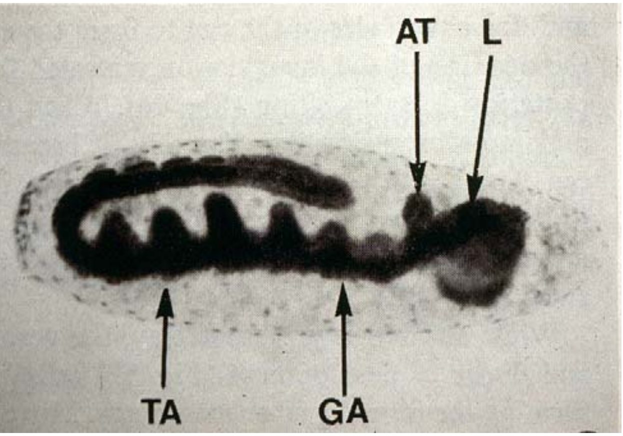


Establishment of embryonic polarity during metazoan development.

Pg. 578 Kimble. “On the basis of the diversity of these mechanisms (i.e., polarity axis and germ cell establishment), the prevailing view has been that each embryo has **differentially employed a handful of common molecular mechanisms to create its own coordinate system**. Research in *Drosophila* has pioneered our understanding of the molecular mechanisms that can establish the body axes in an early embryo. Now, phylogenetic comparisons will tell us which mechanisms are primitive and which have evolved to reinforce, modify, or extend the underlying map. Are the controls that localize translation repression conserved? Are polar granules the ancient set of pattern governance? What links the early controls of axis formation to the later controls of homeobox genes, a highly conserved system that specifies individual regions along the anterior-posterior axis of all known metazoan.”

See counces book, pg. 229 on holometabolan embryology and evolution

Evidence of divergent pathways early



Early Insect Egg

Body plan determined in blastoderm

YES NO

Germ band stage

Phylotypic point for Arthropods. All look alike. Insects, however, possess a head composed of a procephalic region plus 3 gnathal (GA) segments That form the mouth parats, 3 thoracic segments (TA) and 8 abdominal segments

Body plan completed after gastrulation

Long-germ embryos

Short-germ embryos

Where found **Only in most phylogenetically derived orders**

Example *Drosophila*

Grasshoppers

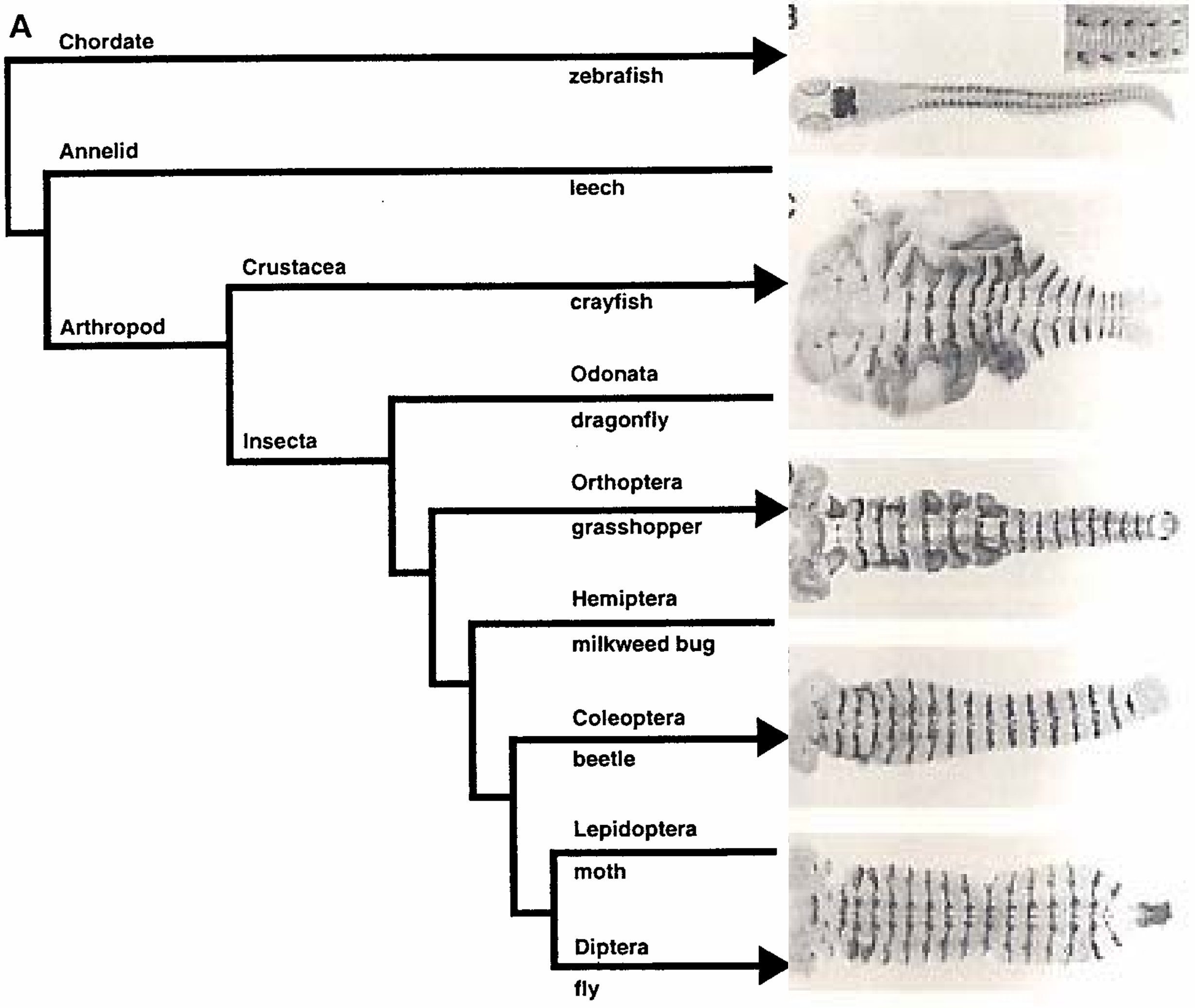
Patel, N.H. 1994. Developmental evolution: insights from studies of insect segmentation. Science vol. 266: 581-589.

pg. 581. “In The Origin of Species, Darwin referred to development and embryology as ‘one of the most important subjects in the whole round of history.’”

Ernest Haeckel. Ontogeny recapitulates phylogeny.

Nelson, G. 1983. Ontogeny, phylogeny, paleontology, and the biogenetic law. Syste. Zool. 27: 324-345.

Tree developed based on the expression of *engrailed* during embryogenesis



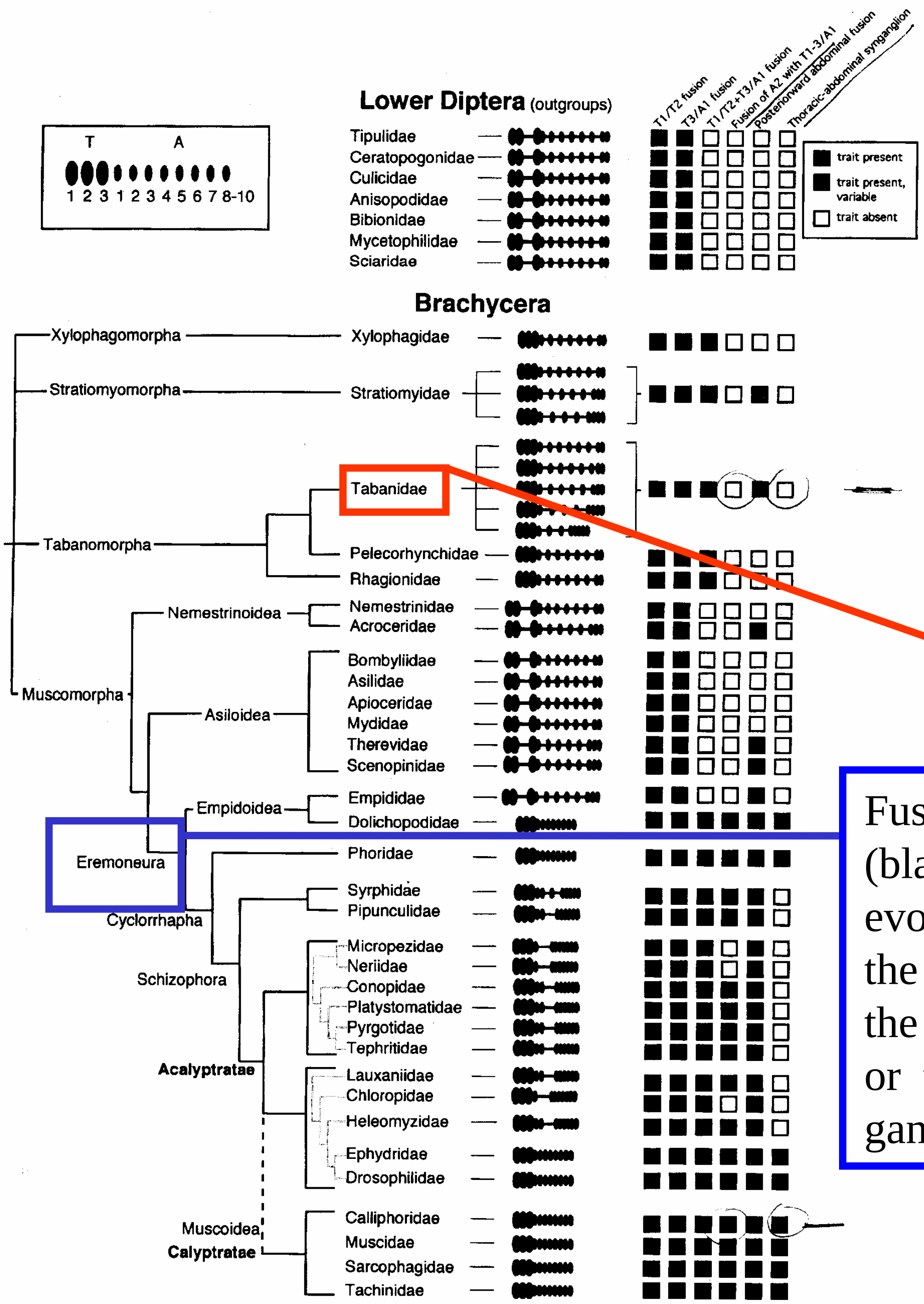
THE NERVOUS SYSTEM-ventral nerve cord

Yeates, D.K., D. J. Merritt, and C.H. Baker. 2002. The adult ventral nerve cord as a phylogenetic character in brachyceran Diptera. Organisms Diversity & Evolution 2: 89-96.

Buschbeck, E.K. 2000. Neurobiological constraints and fly systematics: how different types of neural characters can contribute to a higher-level Dipteran phylogeny. Evolution 54: 888-898.

Looking at CHARACTER SETS

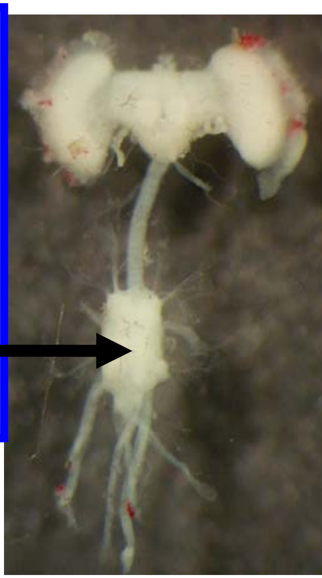
1. Ventral nerve cord arrangement
2. Blood feeding or hematophagy
3. Salivary gland control and innervation



1. Dipteran ganglia are composed of units called neuromeres and the arrangement varies within the phylum
2. Variation within family is uncommon
3. 6 patterns recognized with Brachycera
4. VNC architecture not influenced by body shape
5. Increased neuromere fusion is a characteristic of the Brachycera
6. No Brachycera show less fusion than the lower dipteran outgroups

See following slides

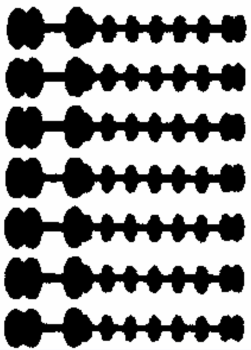
Fusion into a synganglion (black arrow to right) has evolved at least 4 times in the Eremoneura (see photo to the right showing synganglion or thoracico-abdominal ganglion in *Phormia regina*).



6 character states

Lower Diptera (outgroups)

Outgroup pattern

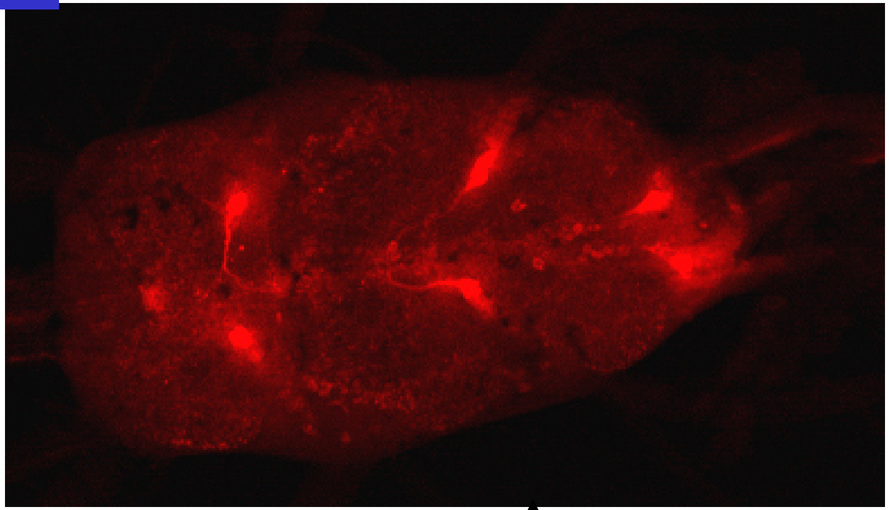


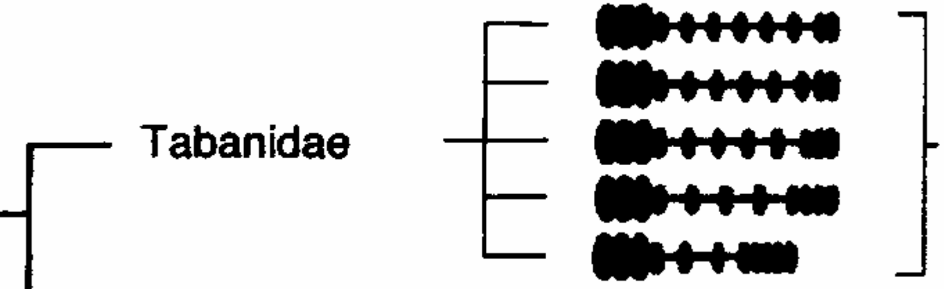
	T1/T2 fusion	T3/A1 fusion	T1/T2+T3/A1 fusion	Fusion of A2 with T1-3/A1	Postenorward abdominal fusion	Thoracic-abdominal synganglion
Tipulidae	■	■	□	□	□	□
Ceratopogonidae	■	■	□	□	□	□
Culicidae	■	■	□	□	□	□
Anisopodidae	■	■	□	□	□	□
Bibionidae	■	■	□	□	□	□
Mycetophilidae	■	■	□	□	□	□
Sciaridae	■	■	□	□	□	□

■ trait present

■ trait present, variable

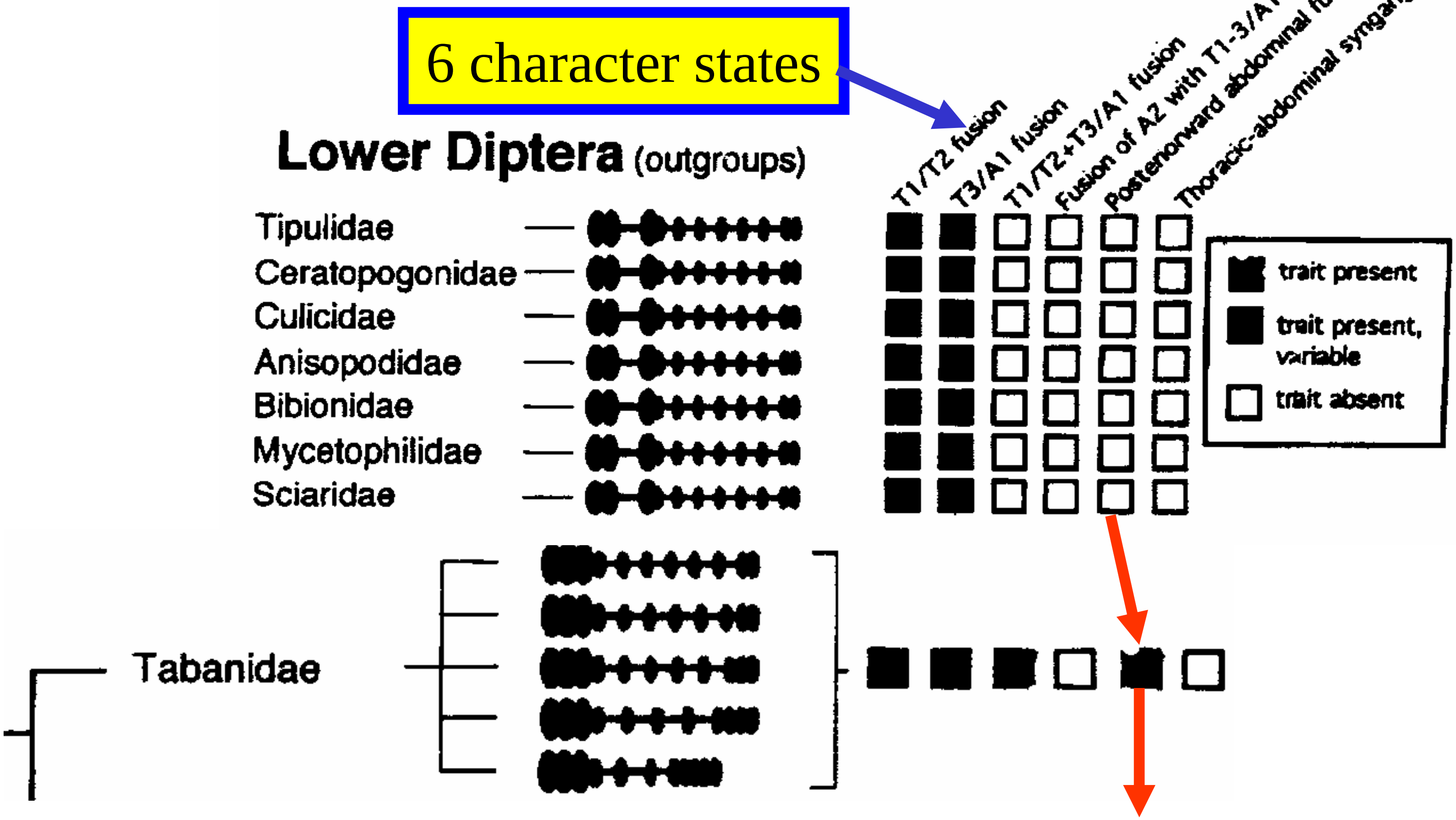
□ trait absent





	T1/T2 fusion	T3/A1 fusion	T1/T2+T3/A1 fusion	Fusion of A2 with T1-3/A1	Postenorward abdominal fusion	Thoracic-abdominal synganglion
Tabanidae	■	■	■	□	■	□

Above shows fusion in *T. nigrovittatus* in T1-T3.
Cells are positive to FMRFamide-like IR



6 character states

Lower Diptera (outgroups)

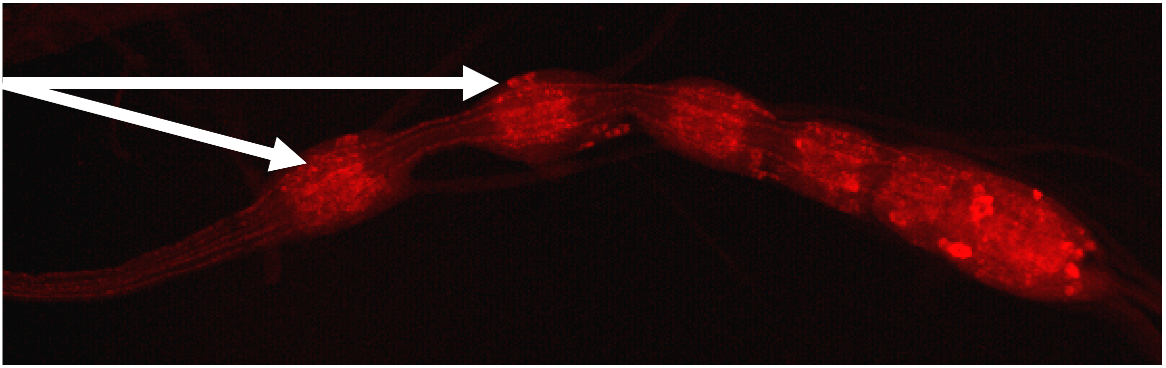
	T1/T2 fusion	T3/A1 fusion	T1/T2+T3/A1 fusion	Fusion of A2 with T1-3/A1	Postenorward abdominal fusio	Thoracic-abdominal syngangli
Tipulidae	■	■	☐	☐	☐	☐
Ceratopogonidae	■	■	☐	☐	☐	☐
Culicidae	■	■	☐	☐	☐	☐
Anisopodidae	■	■	☐	☐	☐	☐
Bibionidae	■	■	☐	☐	☐	☐
Mycetophilidae	■	■	☐	☐	☐	☐
Sciaridae	■	■	☐	☐	☐	☐
Tabanidae	■	■	■	☐	■	☐

■ trait present

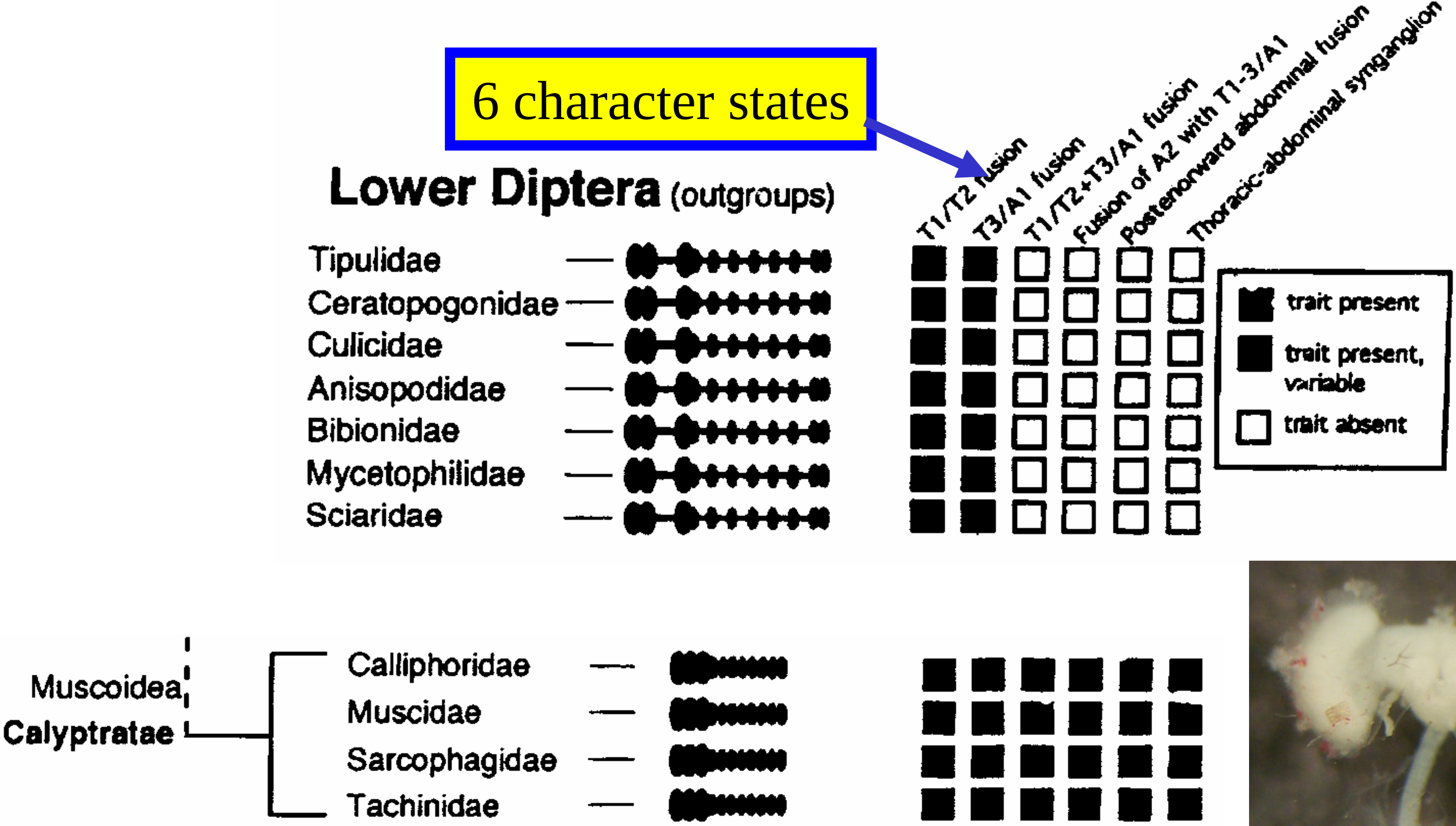
■ trait present, variable

☐ trait absent

Presence of individual neuromeres in the abdomen of ***T. nigrovittatus***. Fluorescence is due to a postive response to **FMRFamide-like IR.**



6 character states



Lower Diptera (outgroups)

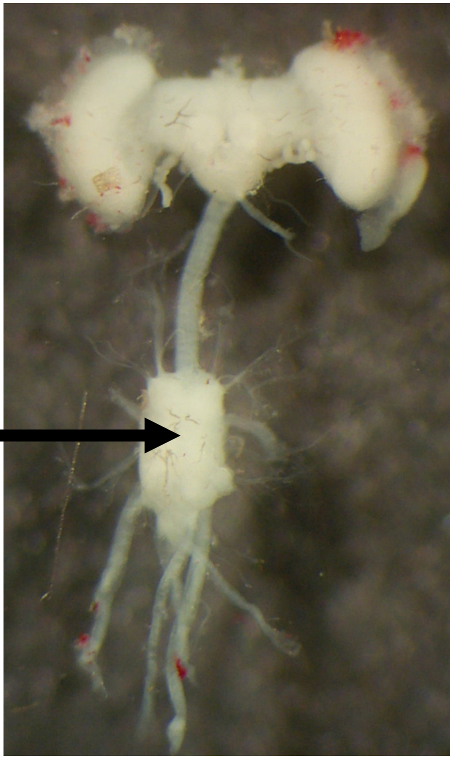
	T1/T2 fusion	T3/A1 fusion	T1/T2+T3/A1 fusion	Fusion of A2 with T1-3/A1	Postenorward abdominal fusion	Thoracic-abdominal synganglion
Tipulidae	■	■	☐	☐	☐	☐
Ceratopogonidae	■	■	☐	☐	☐	☐
Culicidae	■	■	☐	☐	☐	☐
Anisopodidae	■	■	☐	☐	☐	☐
Bibionidae	■	■	☐	☐	☐	☐
Mycetophilidae	■	■	☐	☐	☐	☐
Sciaridae	■	■	☐	☐	☐	☐
Calliphoridae	■	■	■	■	■	■
Muscidae	■	■	■	■	■	■
Sarcophagidae	■	■	■	■	■	■
Tachinidae	■	■	■	■	■	■

■ trait present

■ trait present, variable

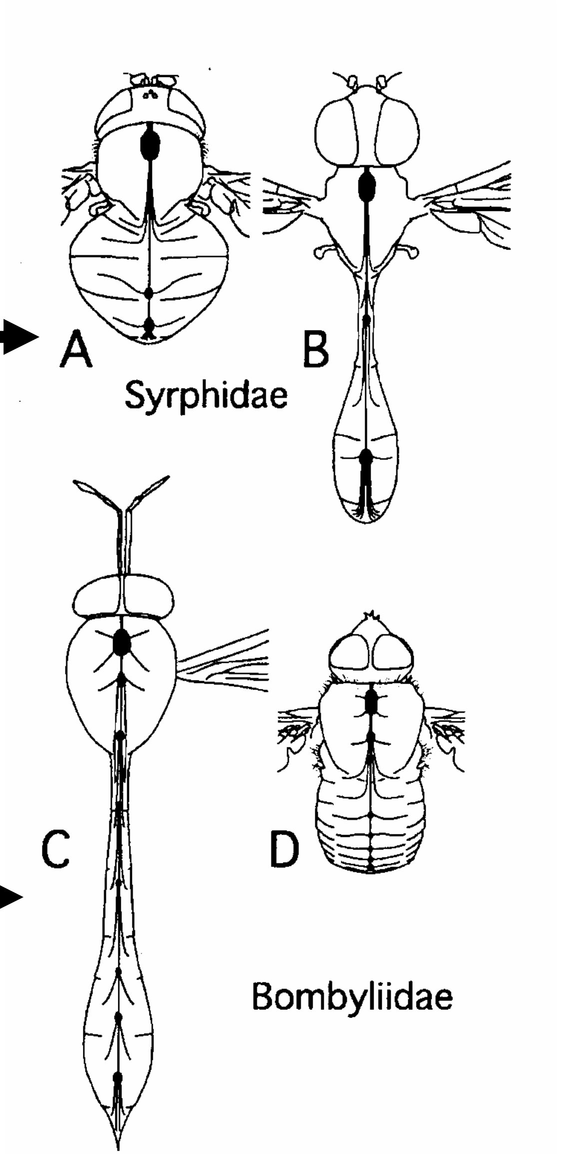
☐ trait absent

Complete fusion to form a thoracic-abdominal synganglion



Fusion into a synganglion (black arrow to right) has evolved at least 4 times, (see photo to the right showing synganglion or thoracico-abdominal ganglion in *Phormia regina*).

VNC architecture not influenced by body shape



Evolution of hematophagy

Rachel Galun
Hebrew University, Jerusalem

Hematophagy, the habit of blood feeding has evolved 17 times in disparate arthropod taxa. In Diptera alone it has evolved independently in 9 families. Most likely hematophagy was exploited by parasites both as a means to find and occupy novel vertebrate host, as well as means for increased motility. In every case, the pre-hematophagous ancestral lineage faced a common set of problems. Mouthparts had to be modified to enable pool or capillary feeding. Yet, it is clear that mouthpart evolution has followed very different paths to derive a common set of phlebotomist tools. Biochemical adaptation took place in the saliva, to overcome problems of hemostasis, vasoconstriction, pain sensation & inflammation. Yet, every blood feeder has enlisted a different biochemical solution, for each of these problems. Adaptation for host location has evolved according to the parasite behavior, special receptors for visual or chemical clues indicating host presence were developed. These clues include light, movement, CO_2, a variety of sweat components and other volatiles emitted by the vertebrate host.

Once on the host, the parasite penetrates or lacerates the host's skin, it salivates and tastes whatever is available. In many cases purine nucleotides provide a positive stimulus for blood gorging. This aspect will be discussed in details, as my own research dealt with it, in a variety of blood sucking invertebrates.

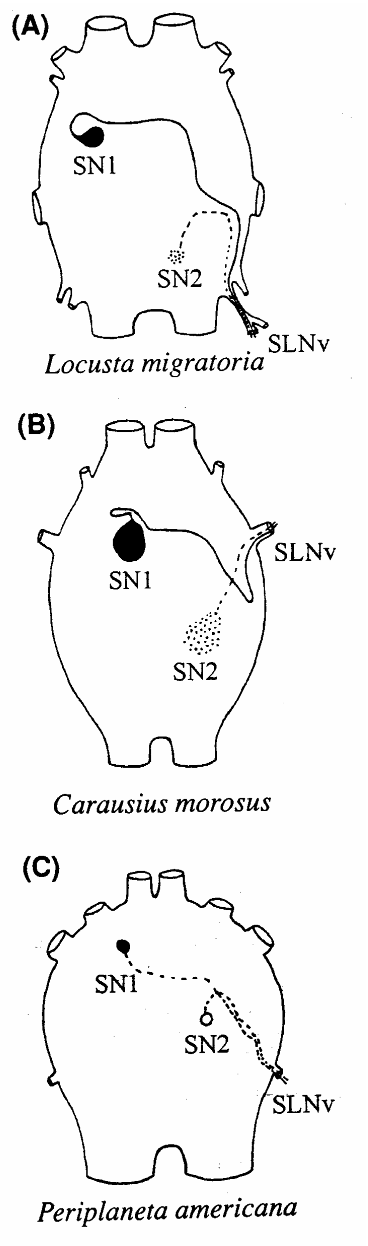
The overriding message in considering all of these adaptations is that no general consistent, morphological, physiological, or biochemical adaptations have been detected among all hematophagous lineages. However, the arthropods when faced with a common set of problems associated with gaining access to vertebrate blood, have taken up many independent but ultimately convergent paths.

Ward et. al. note that hemtophagy evolved 21 times in the Arthropoda

Ward C. Wheeler, Michael Whiting, Quentin D. Wheeler and James M.Carpenter

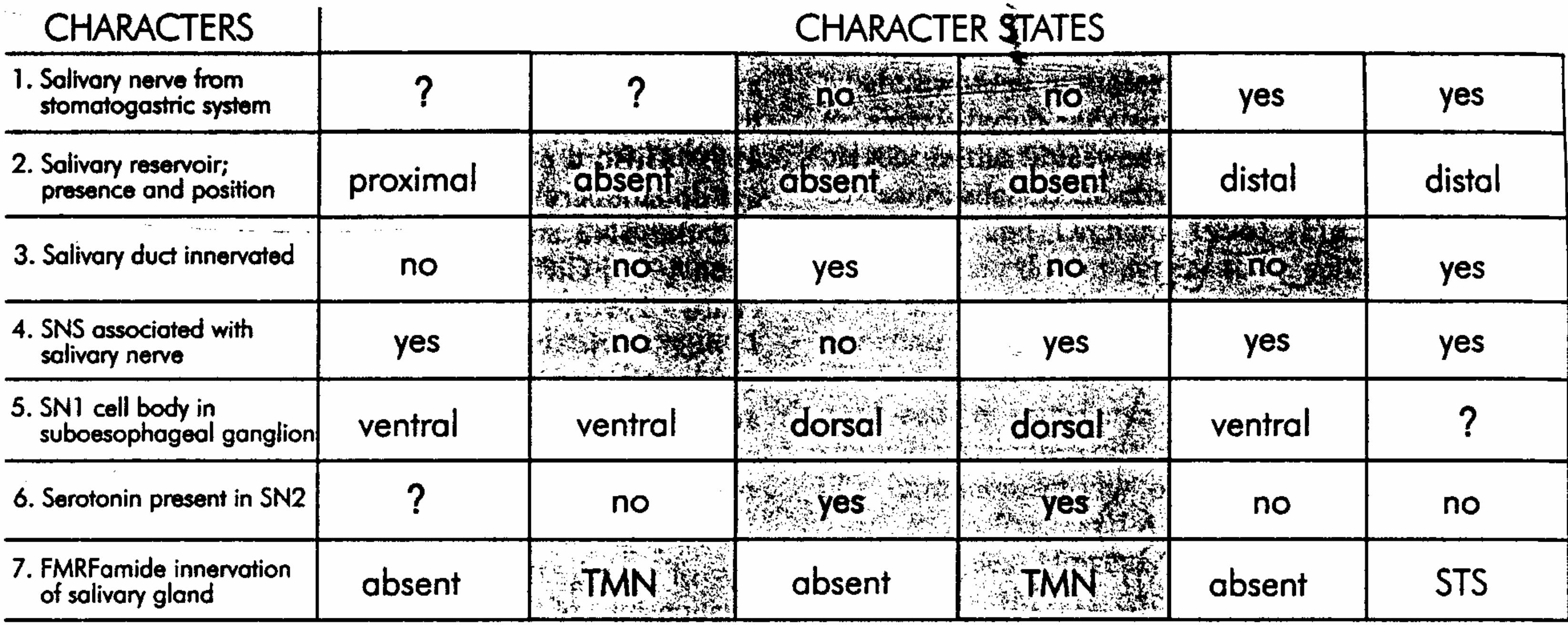
The Phylogeny of the Extant Hexapod Orders: Volume 17, Number 2 (2001), pages 113–169, *Cladistics, Volume 17, Issue 4, December 2001, Pages 403-404*

Ali, D.W. and D. C. Darling. 1998. Neuroanatomy and neurochemistry: implications for the phylogeny of the lower Neoptera. Can. J. Zool. 76: 1623-1633.

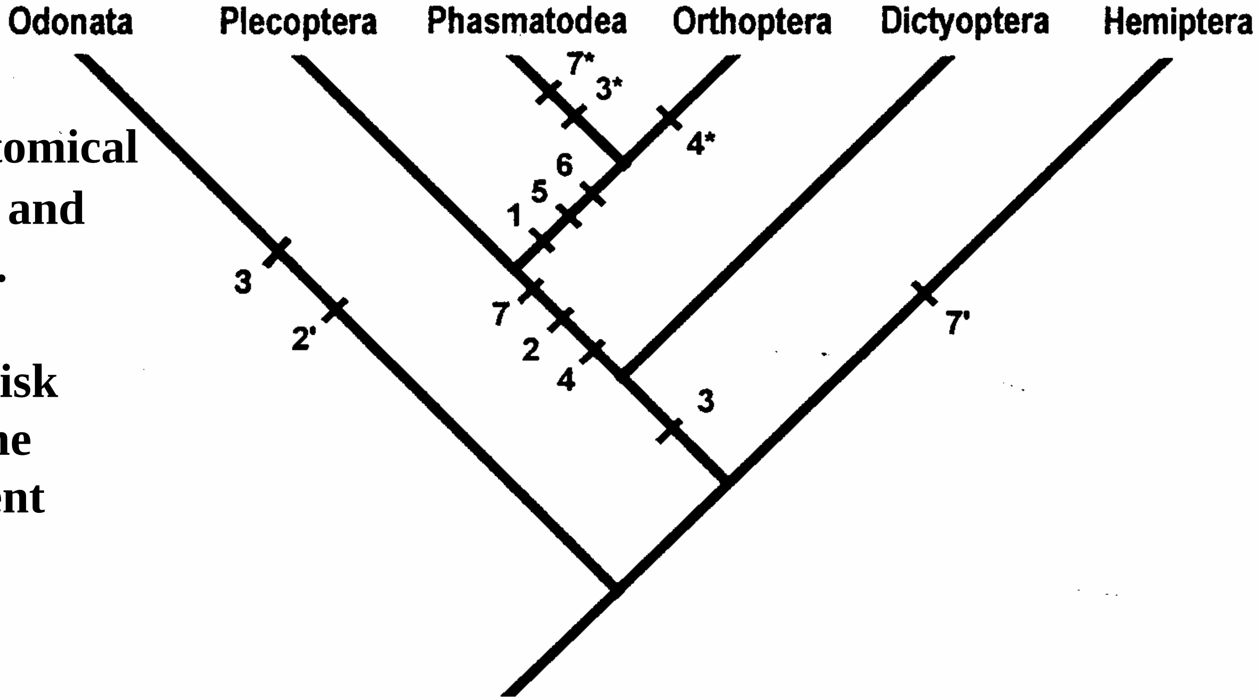


Position of salivary gland neurons within the suboesophageal ganglion of 3 orthopteroid insect species.

Solid areas=cells contain dopamine
Stipple area=cells contain serotonin
Open circle=cells contain unknown phenotype
Solid line=cells on dorsal surface
Broken line=cells on ventral surface
SN1=salivary neuron 1
SN2=Salivary neuron 2
SLNv=salivary nerve



CHARACTERS	CHARACTER STATES					
1. Salivary nerve from stomatogastric system	?	?	no	no	yes	yes
2. Salivary reservoir; presence and position	proximal	absent	absent	absent	distal	distal
3. Salivary duct innervated	no	no	yes	no	no	yes
4. SNS associated with salivary nerve	yes	no	no	yes	yes	yes
5. SN1 cell body in suboesophageal ganglion	ventral	ventral	dorsal	dorsal	ventral	?
6. Serotonin present in SN2	?	no	yes	yes	no	no
7. FMRFamide innervation of salivary gland	absent	TMN	absent	TMN	absent	STS



Data matrix for the neuroanatomical and neurochemical characters and most parsimonious cladogram. Shared derived characters are indicated by shading. An asterisk indicates a reversal and a prime symbol indicates an independent derived state.

Raff, E. C., Popodi, E. M., Sly, B. J., Turner, F. R., Morris, V. B., and Raff, R. A. 2003. Regulatory punctuated equilibrium and convergence in the evolution of developmental pathways in direct-developing sea urchins. Evo. Dev., 5: 478-493.

Zigler, K. S., E. C. Raff, E. Popodi, R. A. Raff, and H. E. Lessios. 2003 Adaptive evolution of bindin in the genus *Heliocidaris* is correlated with the shift to direct development. Evolution. 57: 2293-2302.

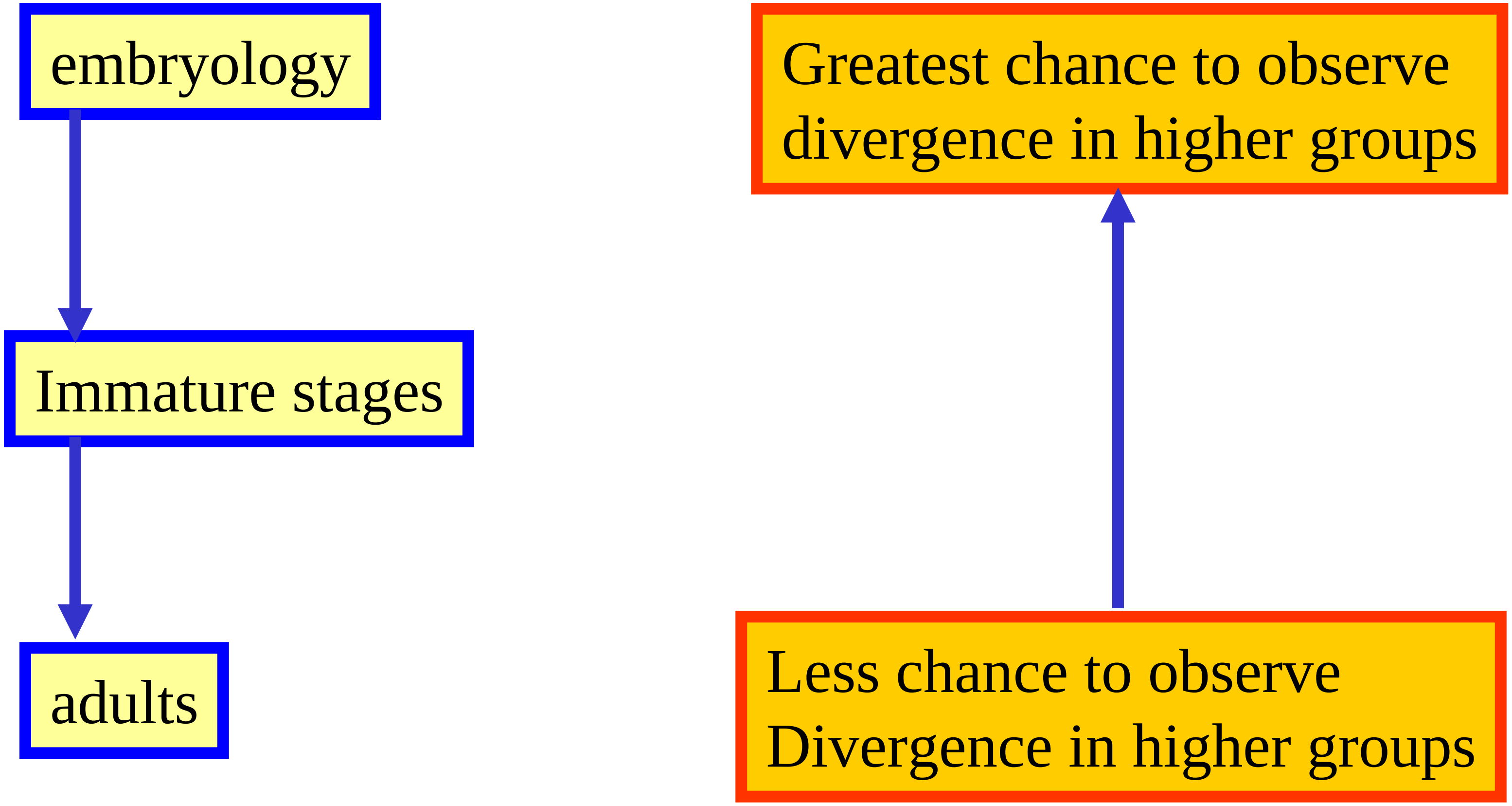
Villinski, J. T., J. C. Villinski, and R. A. Raff. 2002. Convergence in maternal provisioning strategy during developmental evolution of sea urchins. Evolution 56:1764-1775.

Raff, R.A. 1996. *The Shape of Life. Genes, Development, and the Evolution of Animal Form.* Univ. Chicago Press, Chicago.

http://www.bio.indiana.edu/facultyresearch/faculty/RaffR.html

Evolutionary developmental biology -- The evolution of body form requires not only that genes evolve, but that development from egg to adult also evolves. It is now possible to forge an experimental link between evolution and development. My lab studies a pair of closely related Australian sea urchins that differ radically in early development. Part of our work is conducted in Australia, and part in Bloomington. We are focusing on the aspects of gene organization and expression that underlie the differences in cell cleavage, cell lineage, timing of developmental events, and morphogenetic processes between these species. We are exploiting hybrids between the two species as a way of isolating regulatory genes that underlie the evolution of major developmental differences. We have isolated several such genes, and we are studying their roles in the evolution of development by experimentally manipulating the expression of these genes in sea urchin embryos. We are also studying convergence of gene regulatory systems in the independent evolution of developmental mode among in other sea urchin species. Finally, we are studying how larvae originated, and the genic processes that occurred in the origins of larval forms.

Evolution of body plans -- There are 35 animal phyla, each defined by a distinct body plan. These body plans arose just over half a billion years ago, during the Cambrian radiation. Molecular phylogenies show that distinct body plans shared common ancestors: Vertebrates and echinoderms are related. To understand how changes in body plan evolved, we are comparing the radial echinoderm body plan with the linear body plan of vertebrates. We are doing that by examining the expression of patterns of pattern-regulating genes and the processes that form the radially symmetric animal. We are focusing on the central nervous system, which reflects the radial body plan. We have isolated a battery of neural-expressed genes



embryology

Immature stages

adults

Greatest chance to observe divergence in higher groups

Less chance to observe Divergence in higher groups

Gene sequencing
Genomics
Proteonomics