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 that produces the effect we see in an individual group.

“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.

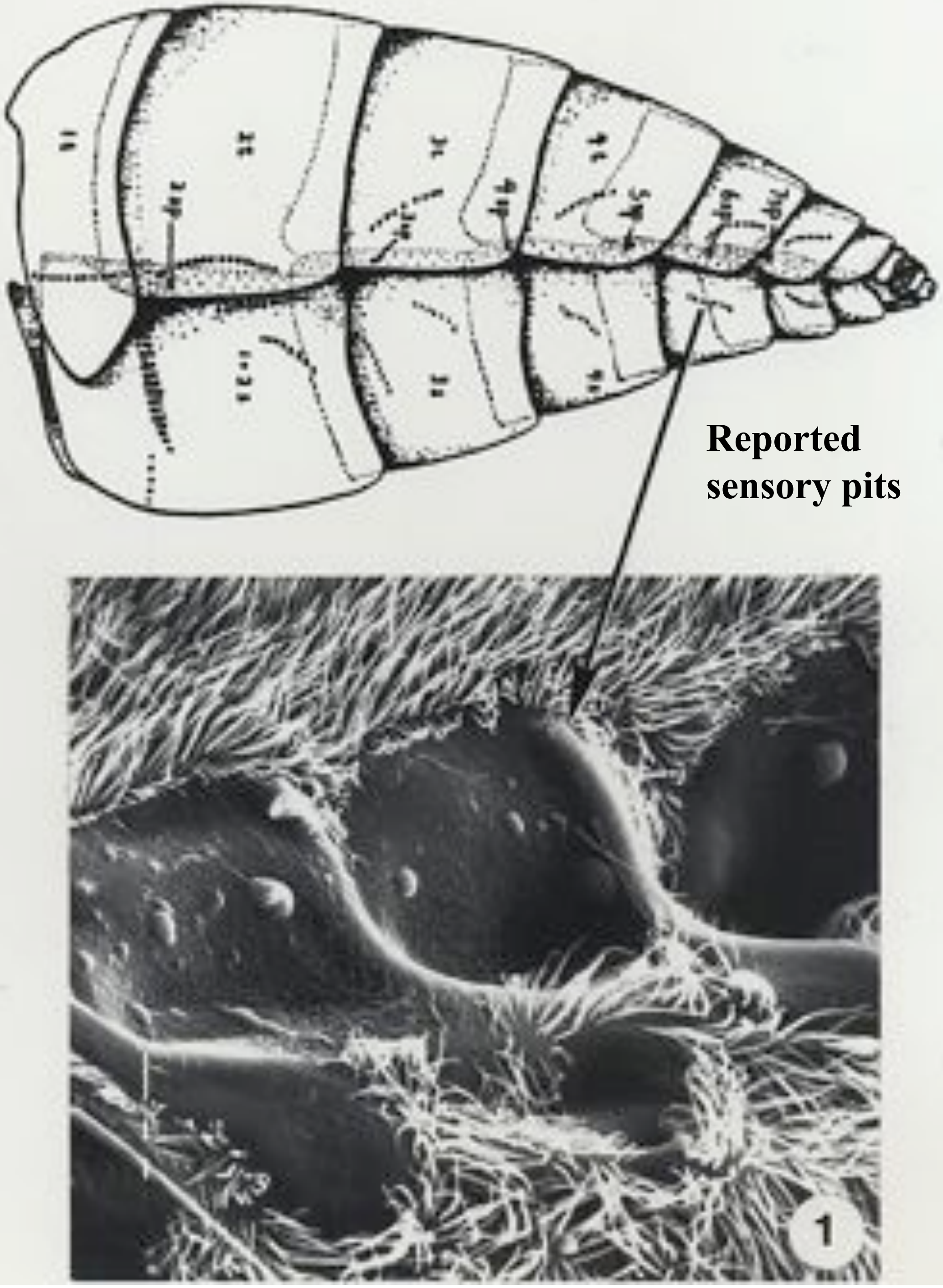
F. Raboudi, M. Mezghani, H. Makni, M. Marrakchi, J. D. Rouault, M. Makni. 2005. Aphid species identification using cuticular hydrocarbons and cytochrome *b* gene sequences. Journal of Applied Entomology 129 (2), 75–80.

2. Cuticular plaques and dipterous larval evolution

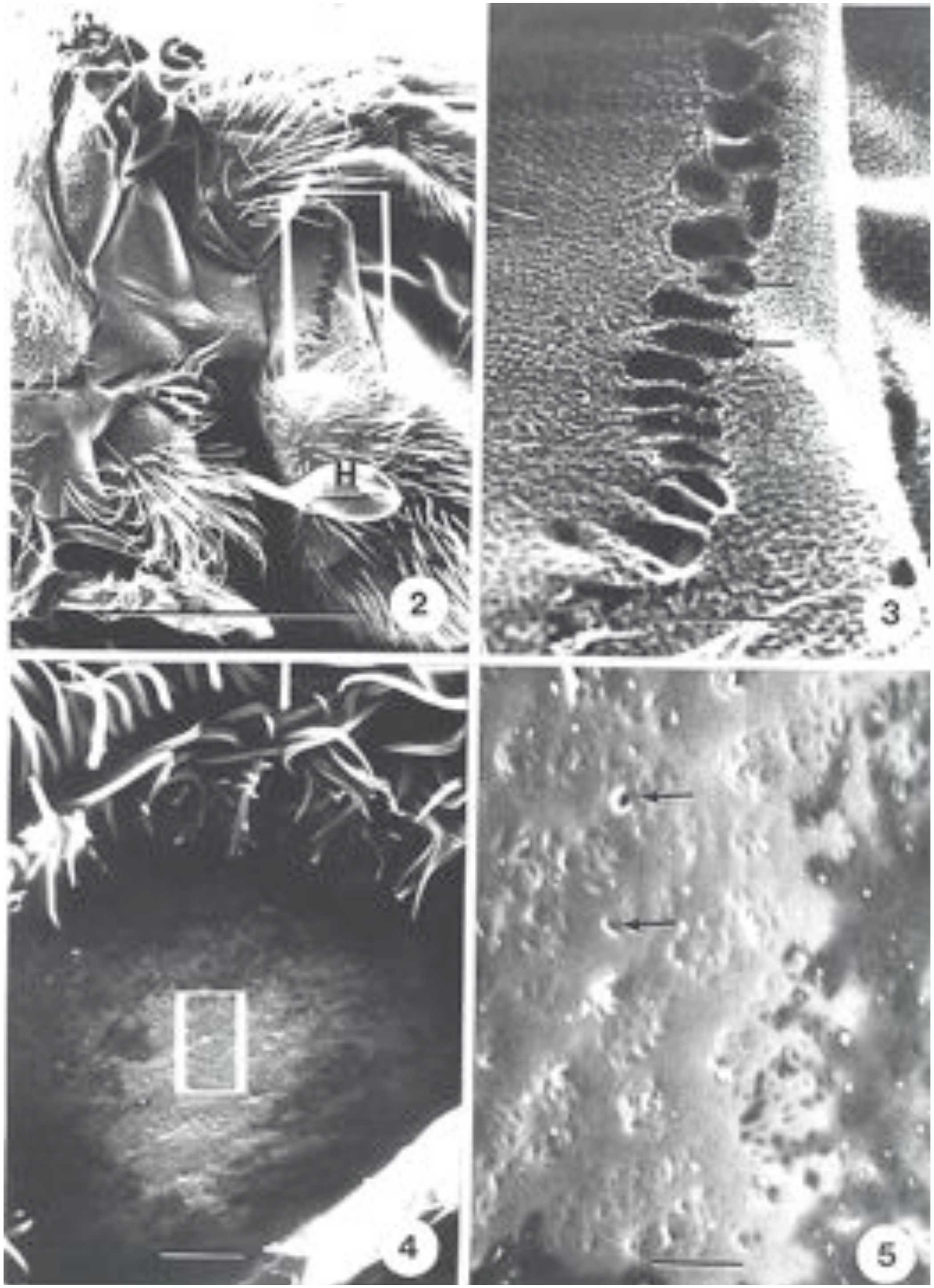
Stoffolano, J.G., Jr., N.E. Woodley and A. Borkent, and L.R.S Yin. 1988. Ultrastructural studies of the abdominal plaques of some Diptera. Ann. Entomol. Soc. Amer. 81: 503-510.

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?**



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?

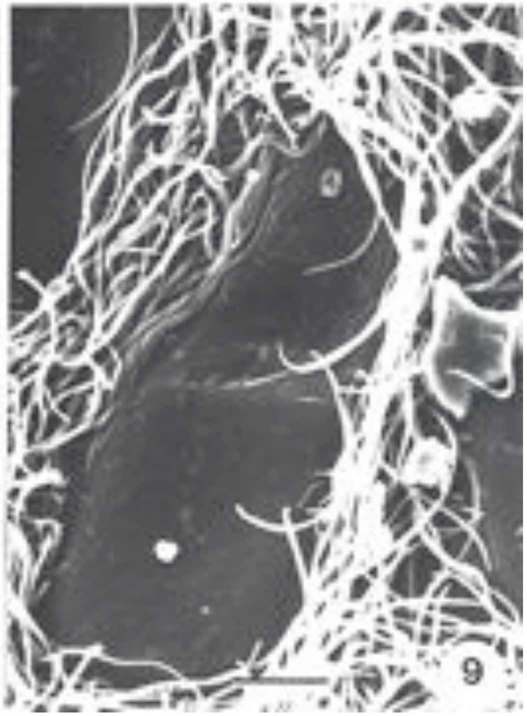
Apiocera barri (Cazier (Apioceridae) showing pits in fig. 8 with higher magnification in fig. 9.

Flower loving flies

6

7

8

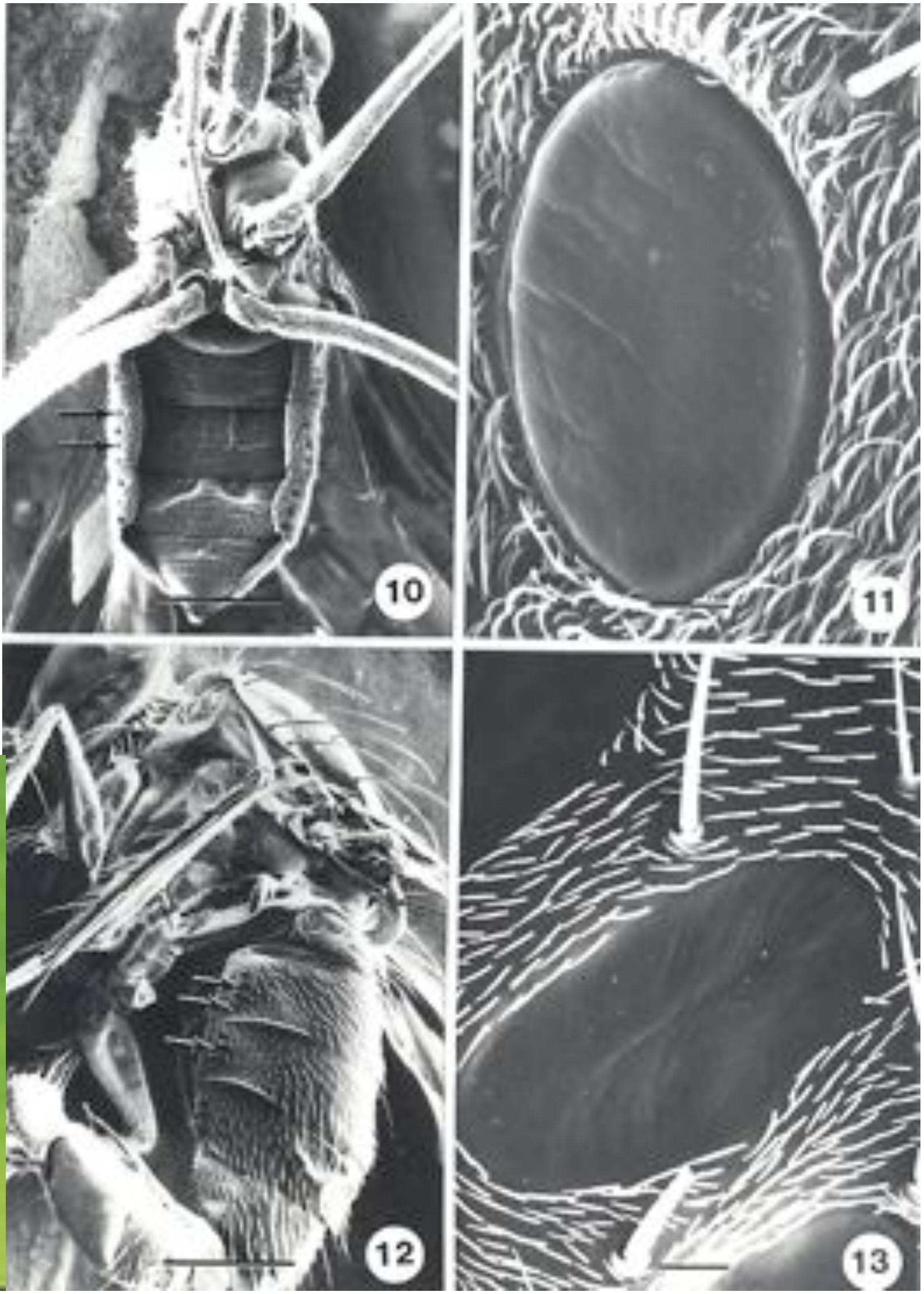


9

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

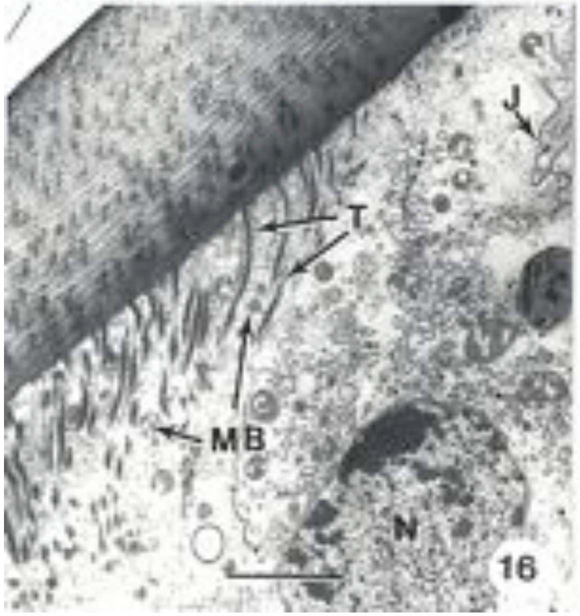
Dolichopus consanguineas (Dolichopodidae) male showing the pits.

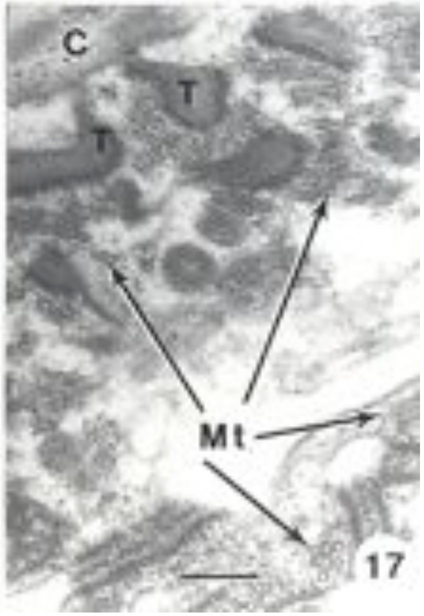
Long-legged flies



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 to move deeper into the soil.





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.”

"Cyclorrhaphan monophyly is well supported with the following synapomorphis: (a) adult abdominal plaques lost (Stoffolano et al. 1988)…"

pg. 412 from Yeates, D. K. and B.M. Wiegmann. 1999. Congruence and controversy: Toward a higher-level phylogeny of Diptera. Ann. Rev. Entomol. 44: 397-428.

This example of studying the cuticular plaques in the Diptera (morphological study) is just one example supporting basic research in one area (morphology or structure) often has an important application in another unrelated area (i.e., phylogeny within the Diptera)

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

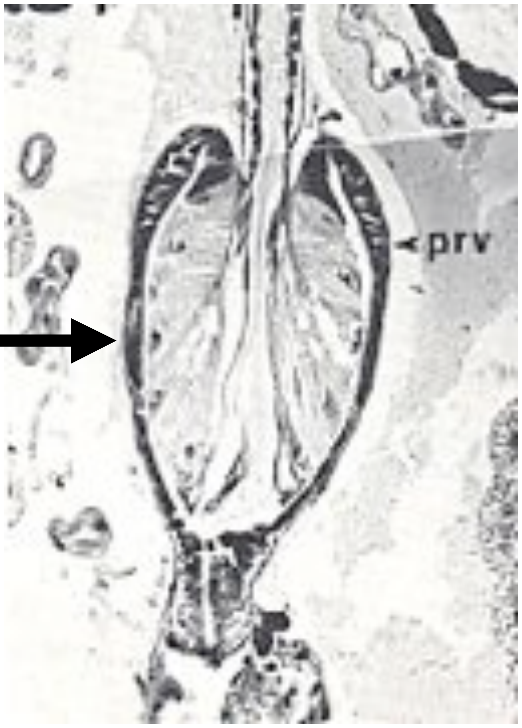
1. Digestive tract in Diptera
2. Germ band
3. Ventral nerve cord in Diptera
4. Development and evolution of bristle patterns in Diptera

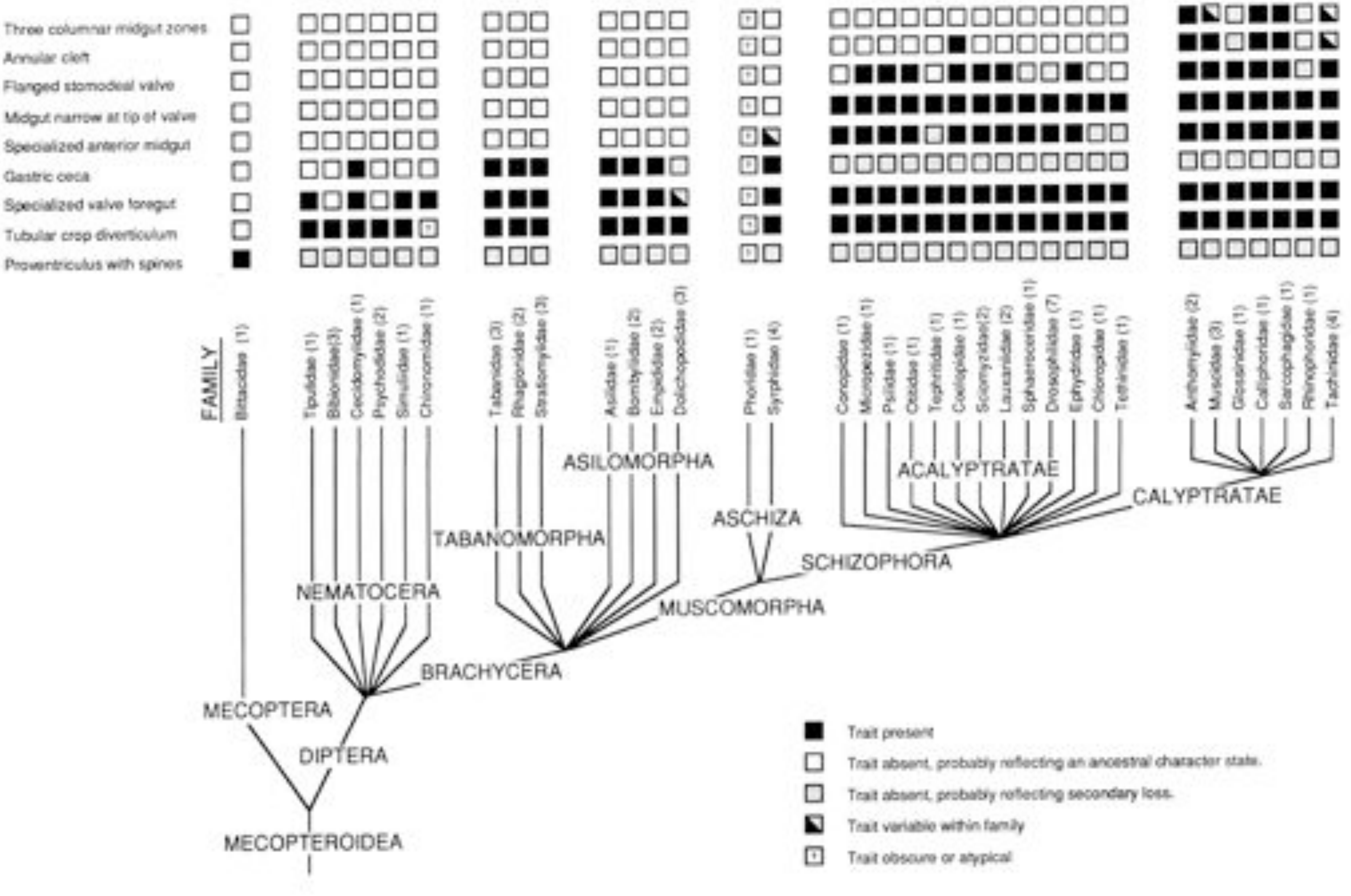
DIGESTIVE SYSTEM

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




Three columnar midgut zones
Annular cleft
Flanged stomodeal valve
Midgut narrow at tip of valve
Specialized anterior midgut
Gastric ceca
Specialized valve foregut
Tubular crop diverticulum
Proventriculus with spines
FAMILY
Bittacidae (1)
Tipulidae (1)
Bibionidae(3)
Cecidomyiidae (1)
Psychodidae (2)
Simuliidae (1)
Chironomidae (1)
Tabanidae (3)
Rhagionidae (2)
Stratiomyidae (3)
Asilidae (1)
Bombyliidae (2)
Empididae (2)
Dolichopodidae (3)
Phoridae (1)
Syrphidae (4)
Conopidae (1)
Micropezidae (1)
Psilidae (1)
Otitidae (1)
Tephritidae (1)
Coelopidae (1)
Sciomyzidae(2)
Lauxaniidae (2)
Sphaeroceridae (1)
Drosophilidae (7)
Ephydridae (1)
Chloropidae (1)
Tethinidae (1)
Anthomyiidae (2)
Muscidae (3)
Glossinidae (1)
Calliphoridae (1)
Sarcophagidae (1)
Rhinophoridae (1)
Tachinidae (4)
ASILOMORPHA
ACALYPTRATAE
CALYPTRATAE
ASCHIZA
TABANOMORPHA
SCHIZOPHORA
NEMATOCERA
MUSCOMORPHA
BRACHYCERA
MECOPTERA
DIPTERA
MECOPTEROIDEA
■ Trait present
□ Trait absent, probably reflecting an ancestral character state.
▨ Trait absent, probably reflecting secondary loss.
◩ Trait variable within family
? Trait obscure or atypical

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.

1. Are the mechanisms conserved?
2. Are they extremely different? and
3. What are their evolutionary histories?

INSECT PRE-EMBRYONIC DEVELOPMENT

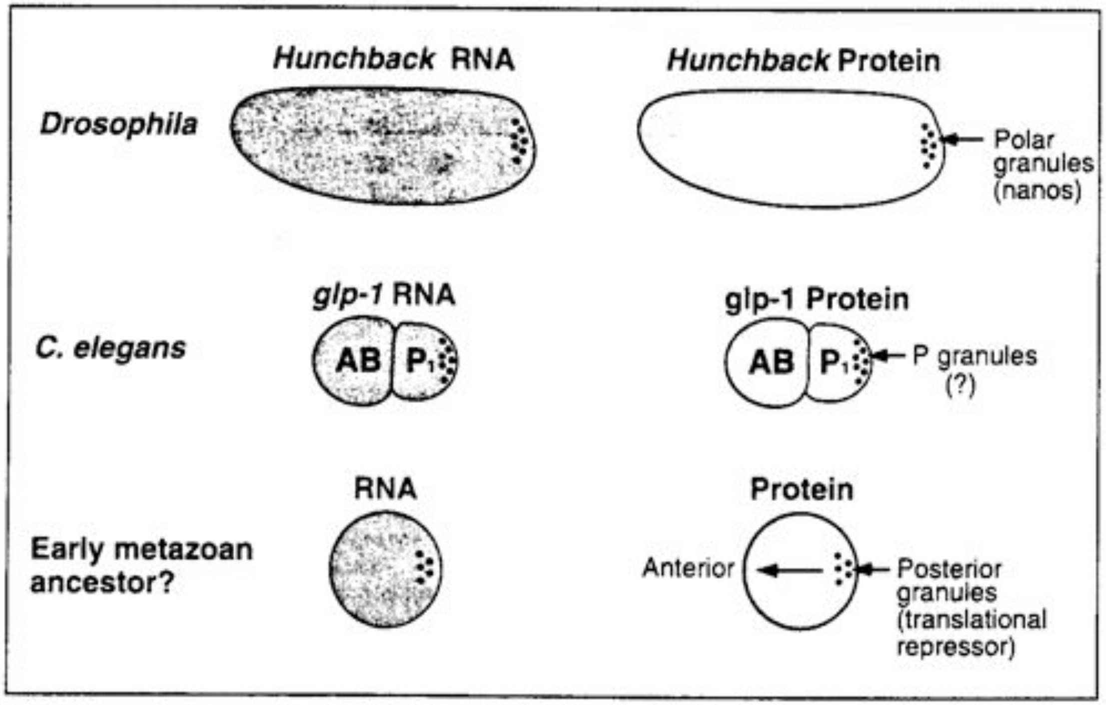
CHARACTER STATES

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."



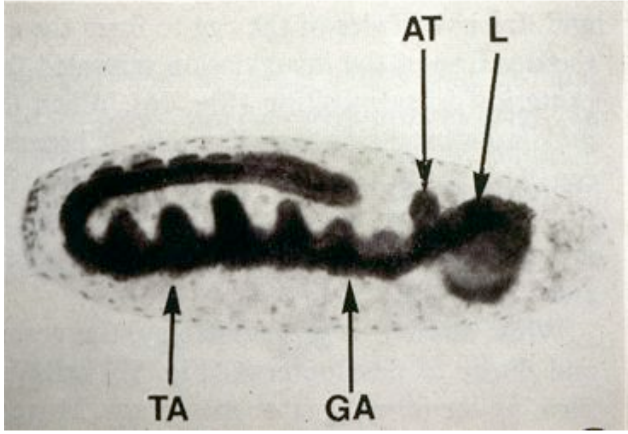
Establishment of embryonic polarity during metazoan development.

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.

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 parts, 3 thoracic segments (TA) and 8 abdominal segments

Long-germ embryos

Body plan completed after gastrulation

Short-germ embryos

Where found Only in most phylogenetically derived orders

Example *Drosophila*

Grasshoppers

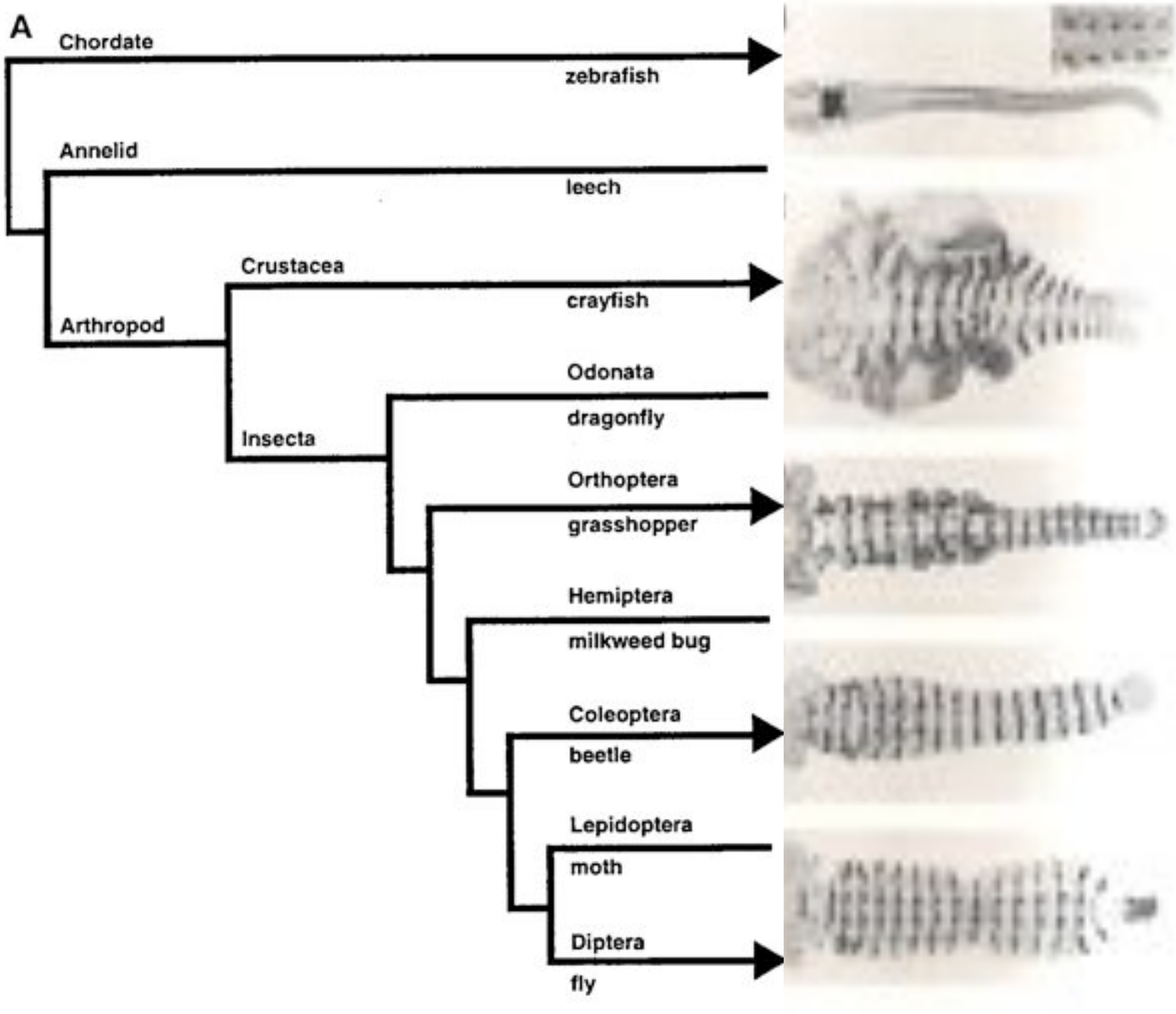
Patel, N.H. 1994. Developmental evolution: insights from studies of insect segmentation. Science vol. 266: 581-589.

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

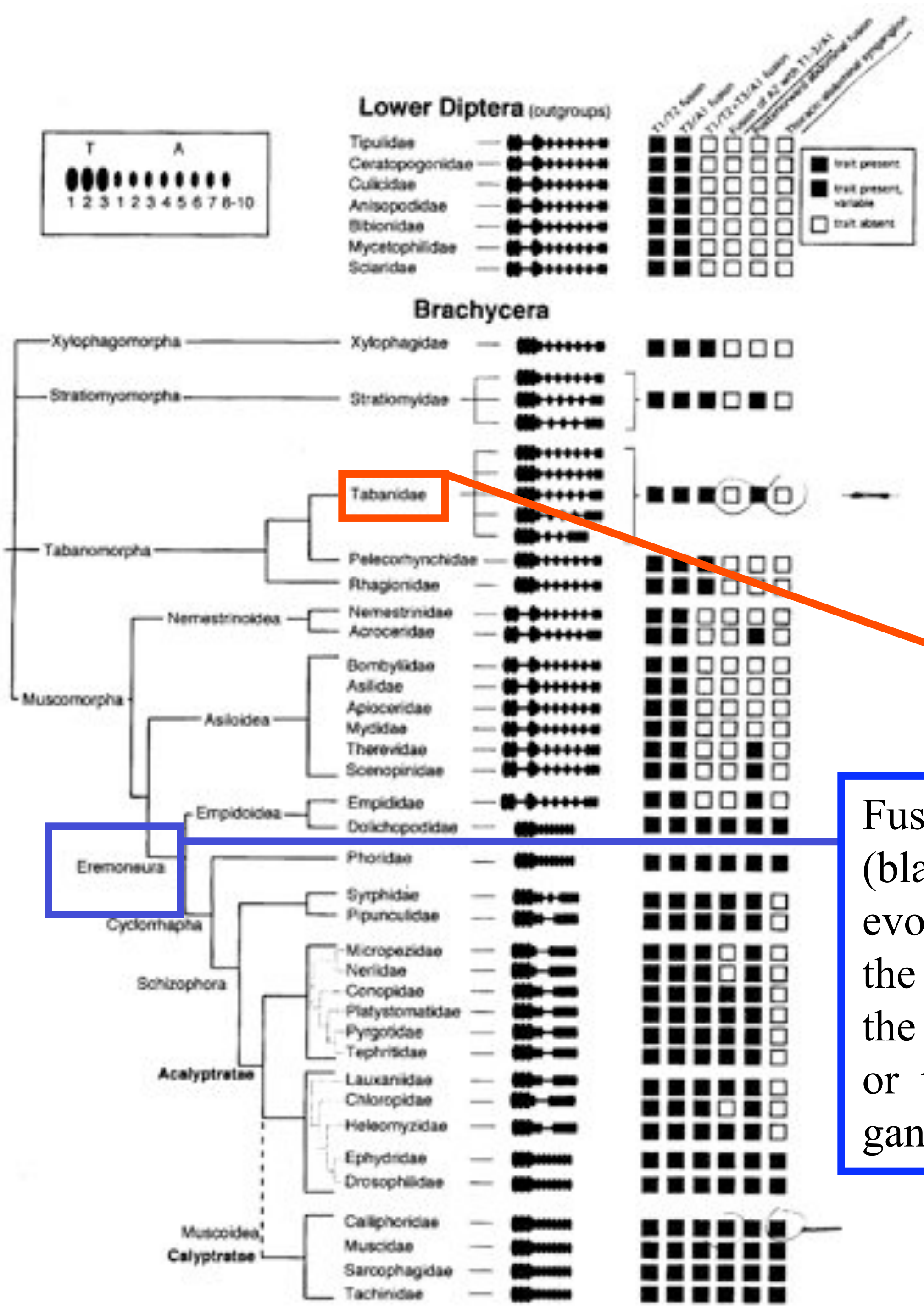
Harzsch, S. 2006. Neurophylogeny: Architecture of the nervous system and a fresh view on arthropod phylogeny. Integrative and Comparative Biology 46(2): 162-194.

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

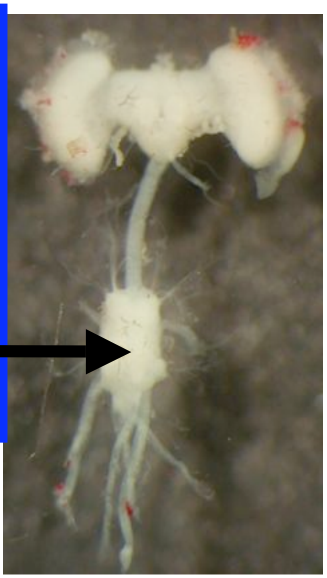
1. Ventral nerve cord arrangement
2. Blood feeding or hematophagy
3. Salivary gland control and innervation
4. Bristles (Chaetotaxy in Diptera)
5. Type of ovariole



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

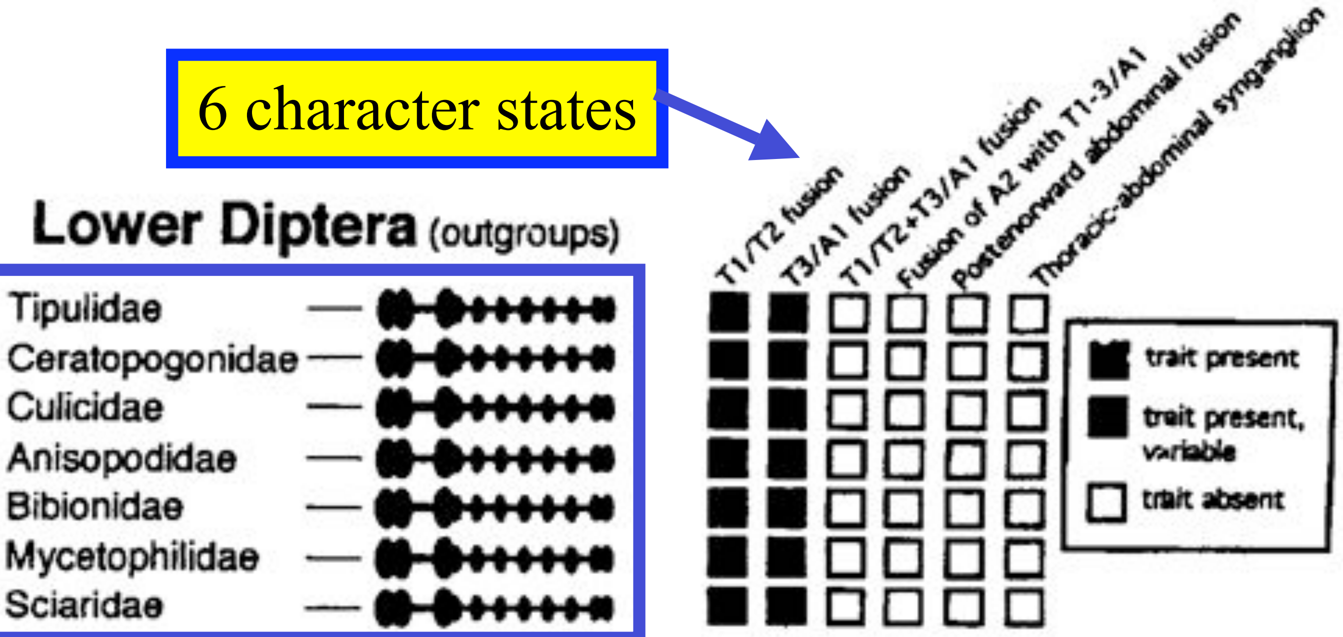
See following slides

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*).

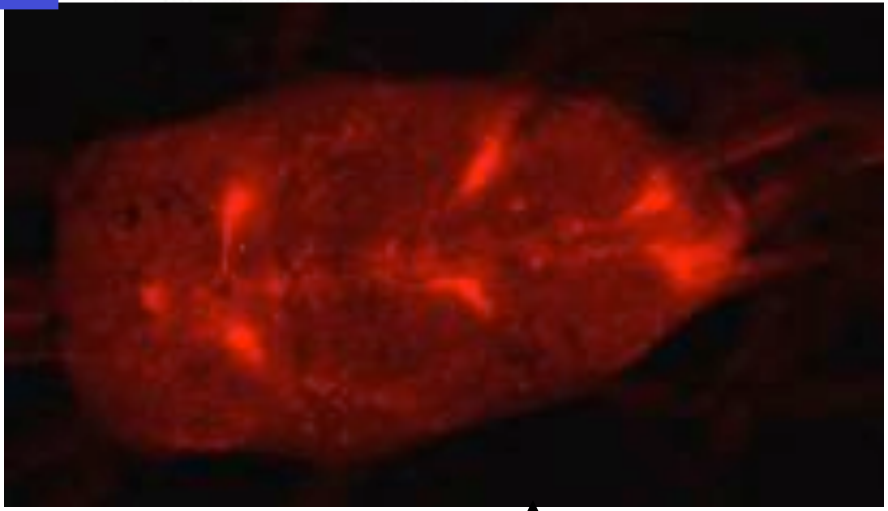


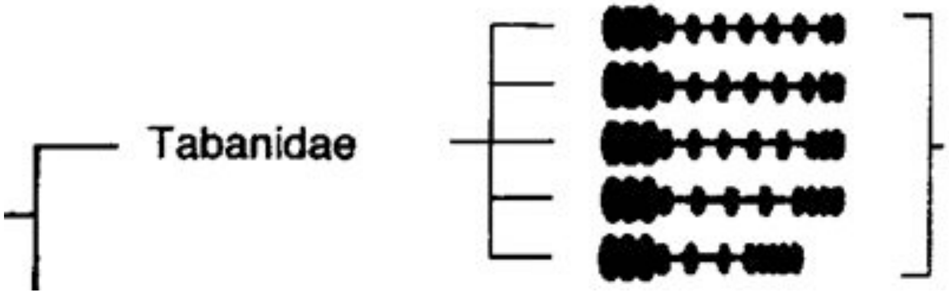
6 character states

Outgroup pattern



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

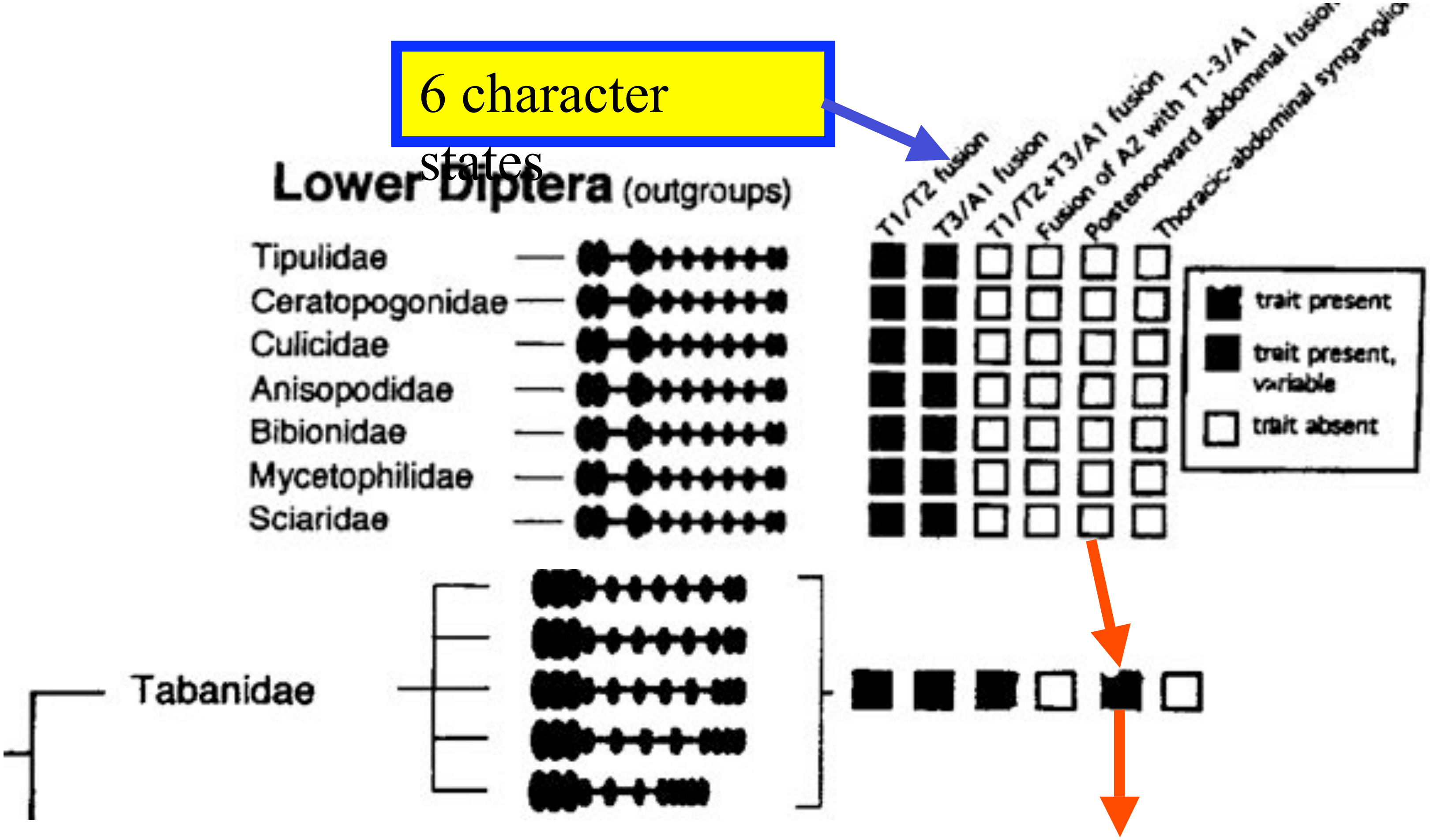




■	■	■	□	■	□

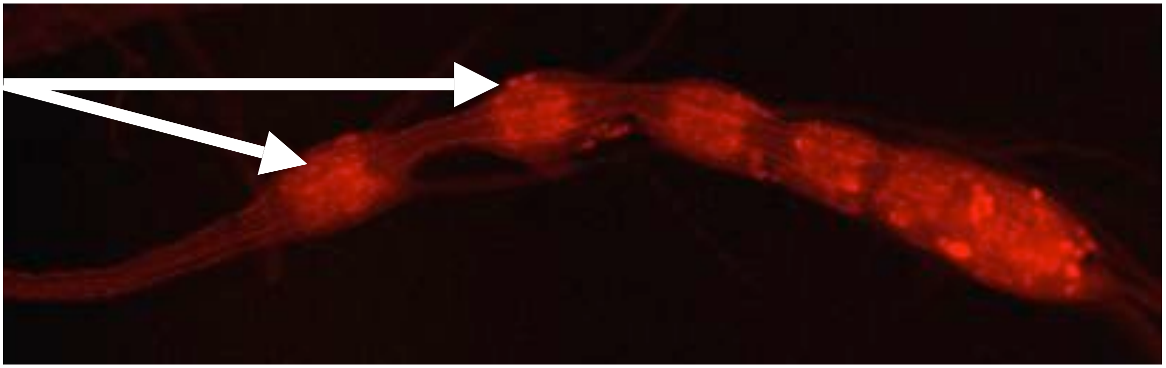
Above shows fusion in *T. nigrovittatus* in T1-T3. Cells are positive to FMRFamide-like IR

6 character states

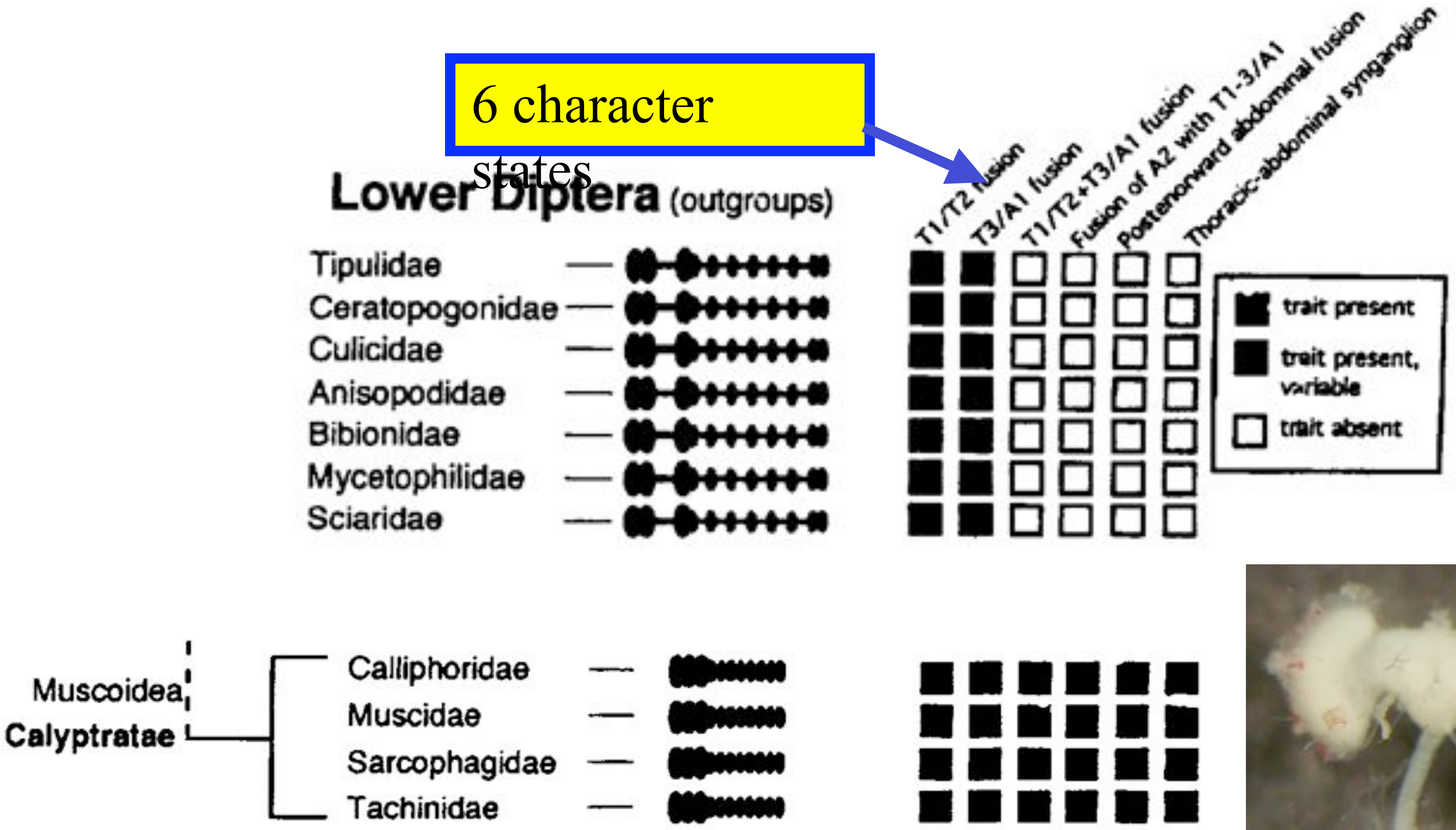


	T1/T2 fusion	T3/A1 fusion	T1/T2+T3/A1 fusion	Fusion of A2 with T1-3/A1	Postenorward abdominal fusio	Thoracic-abdominal syngangli
Tipulidae	■	■	□	□	□	□
Ceratopogonidae	■	■	□	□	□	□
Culicidae	■	■	□	□	□	□
Anisopodidae	■	■	□	□	□	□
Bibionidae	■	■	□	□	□	□
Mycetophilidae	■	■	□	□	□	□
Sciaridae	■	■	□	□	□	□
Tabanidae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

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

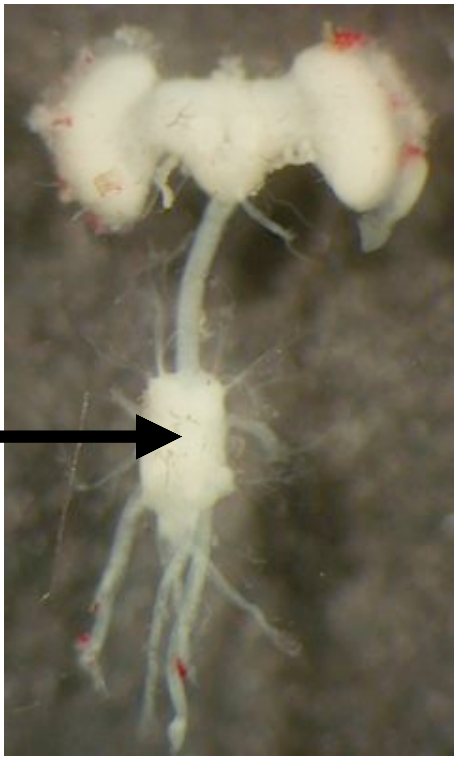


6 character states



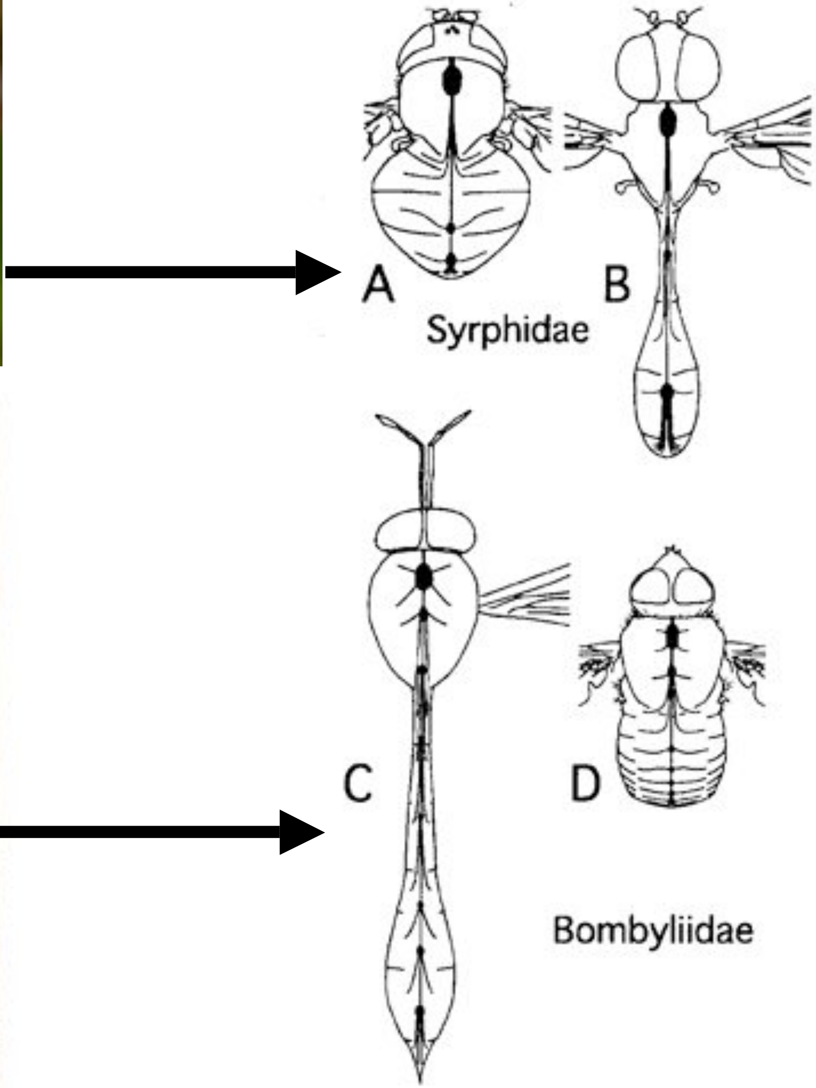
	T1/T2 fusion	T3/A1 fusion	T1/T2+T3/A1 fusion	Fusion of A2 with T1-3/A1	Posterorward abdominal fusion	Thoracic-abdominal synganglion
Tipulidae	■	■	☐	☐	☐	☐
Ceratopogonidae	■	■	☐	☐	☐	☐
Culicidae	■	■	☐	☐	☐	☐
Anisopodidae	■	■	☐	☐	☐	☐
Bibionidae	■	■	☐	☐	☐	☐
Mycetophilidae	■	■	☐	☐	☐	☐
Sciaridae	■	■	☐	☐	☐	☐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

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



Gene expression's role in determining bristle patterns in flies

Simpson, P, R. Woehl and K. Usul. 1999. Review article: The development and evolution of bristle patterns in Diptera. Development 126: 1349-1364.

The following set of slides on bristle determination in the Diptera are taken from the article below:

Simpson, P. and S. Marcellini. 2006. The origin and evolution of stereotyped patterns of macrochaetes on the nota of cyclorraphous Diptera. Heredity 97: 148-156.

"…MACROCHAETES MAY HAVE ARISEN IN THE LINEAGE THAT LED TO THE BRACHYCERA."

Chaetotaxy in the Diptera

THE ORIGIN OF STEREOTYPED PATTERNS FOR BRISTLES INTHE DIPTERA IS BASED ON A FOUR ROW BASIC PLAN

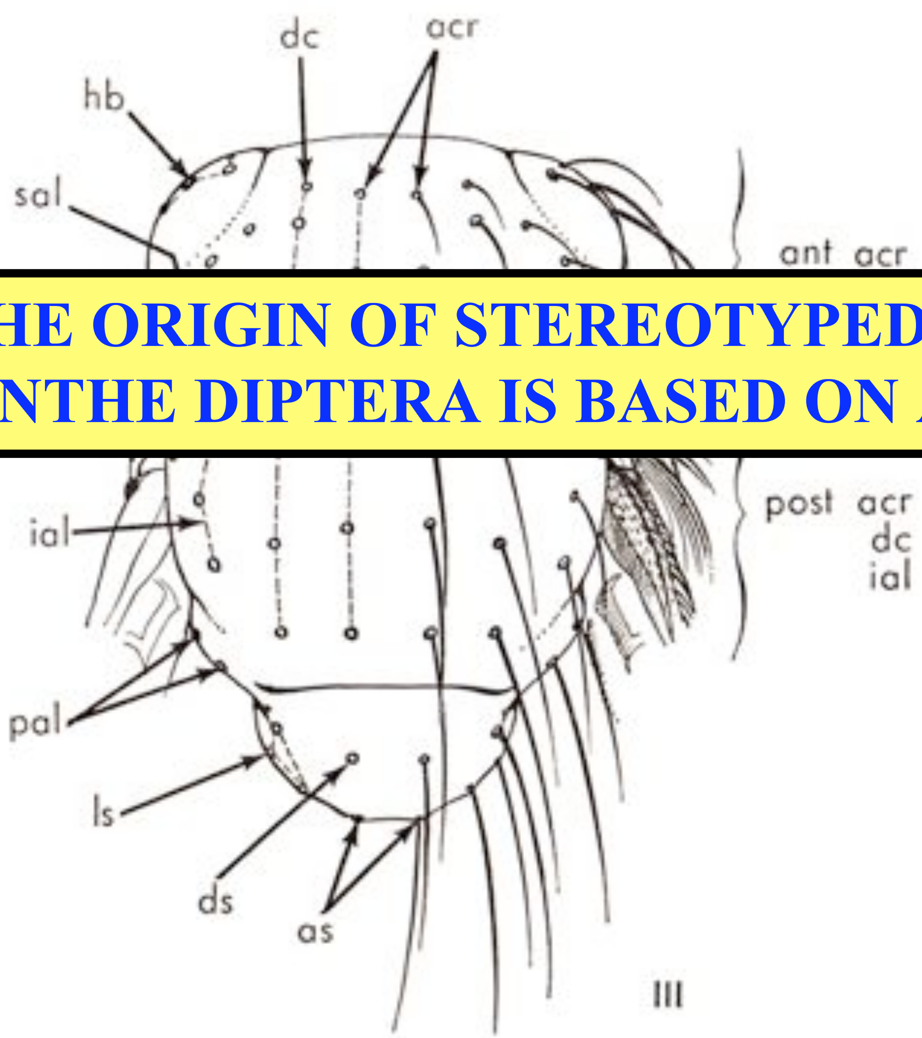


FIG. III. Chaetotaxy of thorax (*Phaenicia sericata*, dorsal view)

acr = acrostical bristles
as = apicoscutellar bristles
ds = discoscutellar bristles
dc = dorsocentral bristles
hb = humeral bristles
ial = intraalar bristles
ls = lateroscutellar bristles
mplb = mesopleural bristles
npb = notopleural bristles
pal = postalar bristles
sal = supraalar bristles

Science 2000. 287 (5461): 2229-2234.

Richard G. Walker,[1] Aarron T. Willingham,[1] Charles S. Zuker[2*]

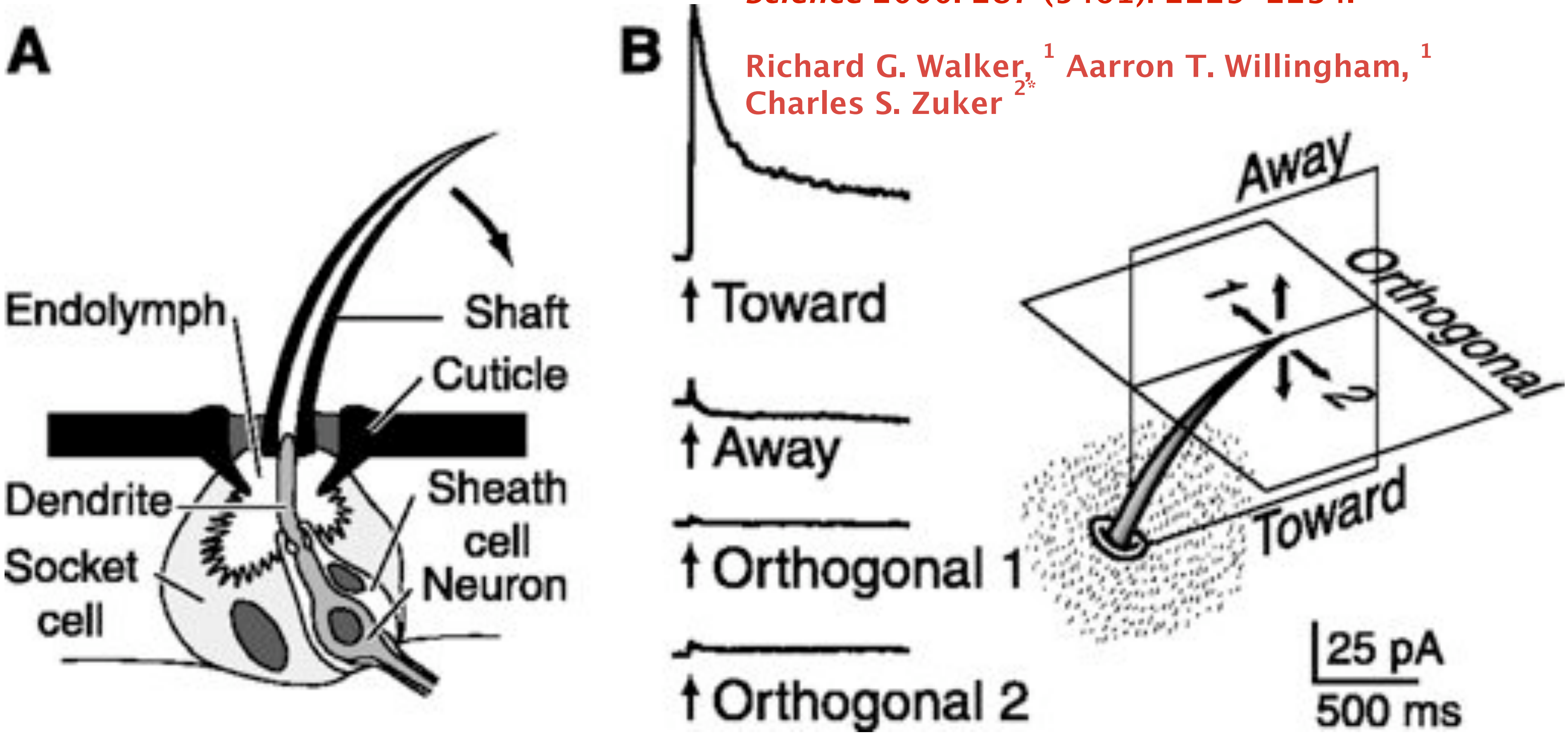
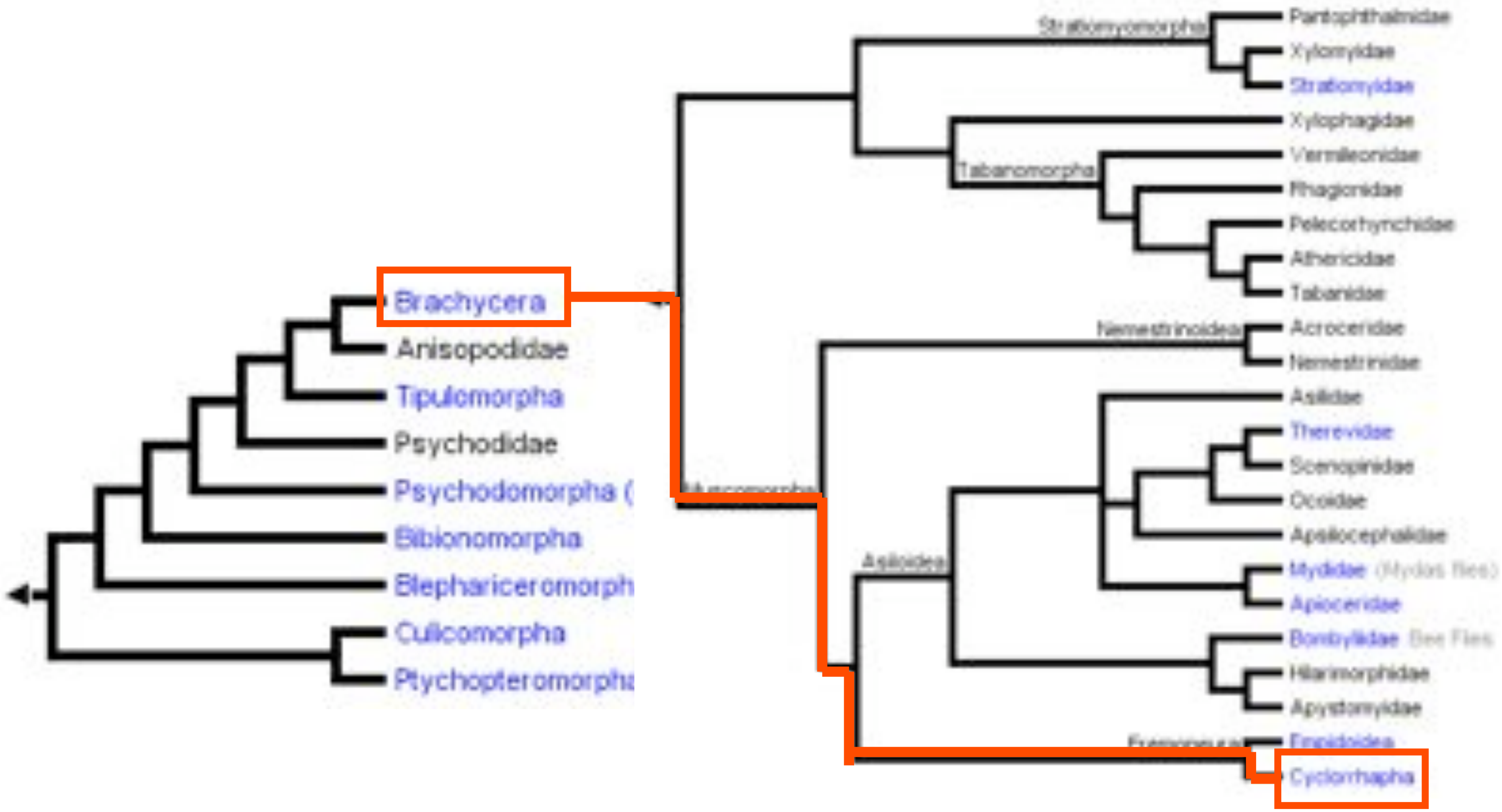
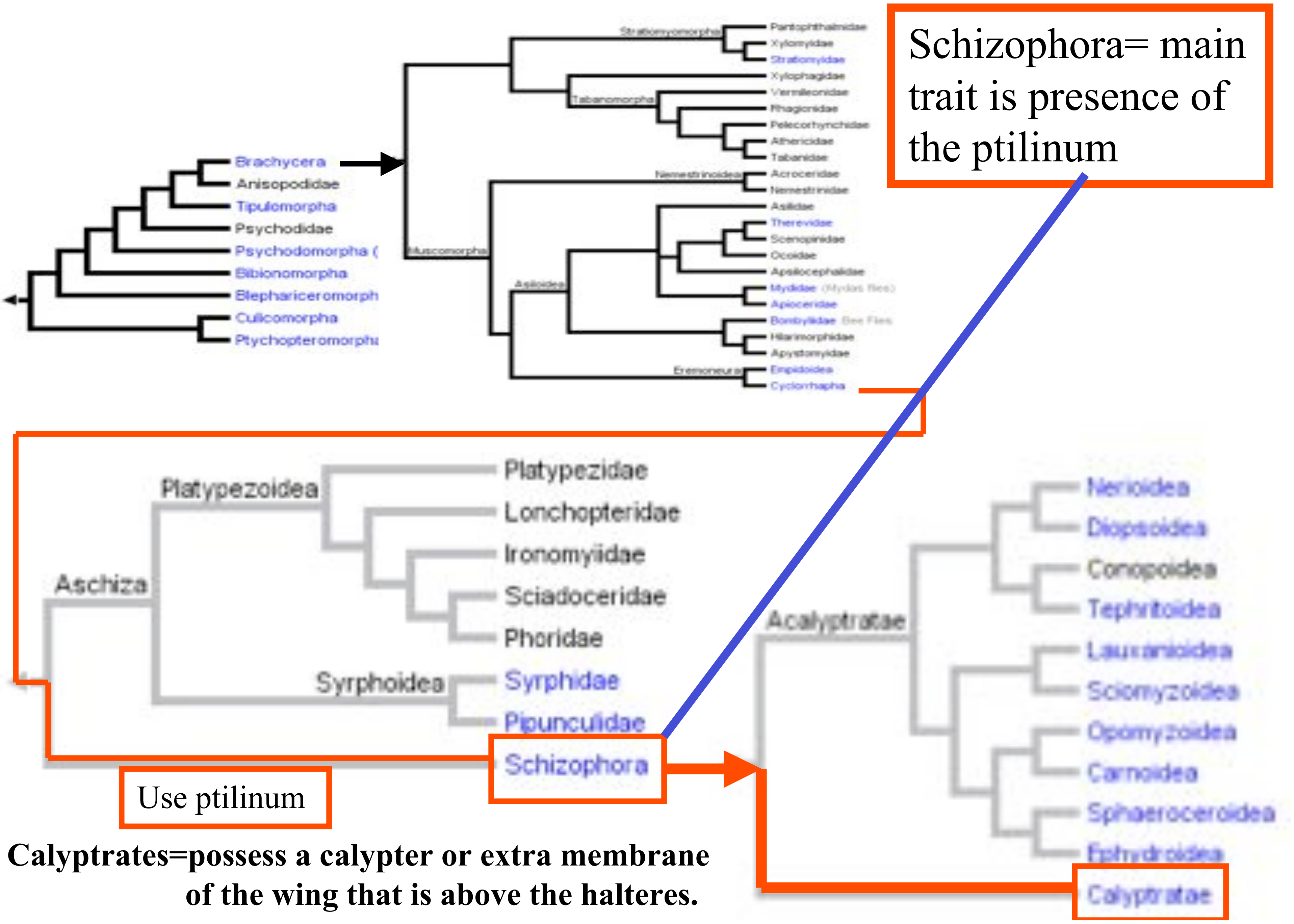


Figure 1. (A) Diagram of a *Drosophila* mechanoreceptor bristle. The bristle sensory organ is composed of a hollow hair shaft and three cells: the socket cell, the sheath cell, and a ciliated mechanosensory neuron (19). The dendritic tip resides in an unusual high-K^+ endolymph, which creates a TEP of +40 mV, which in turn provides a large (~120-mV) driving voltage into the neuron. Displacement of the shaft compresses the dendritic tip and opens the transduction channels. Clipping the hair shaft and placing a recording electrode over the tip allows electrical access to the underlying neuron. (B) Directional sensitivity of a ventral notopleural bristle. Step stimuli of 20 µm were applied in each of four directions: toward and away from the body of the fly and in the two orthogonal directions depicted. Displacements toward the body of the fly elicited a robust 100-pA transient current, whereas stimuli away from the fly or



Brachycera=Those flies with short antennae. Larvae mostly predaceous. Non-cyclorrhaphan adults have muscle plaque remains.

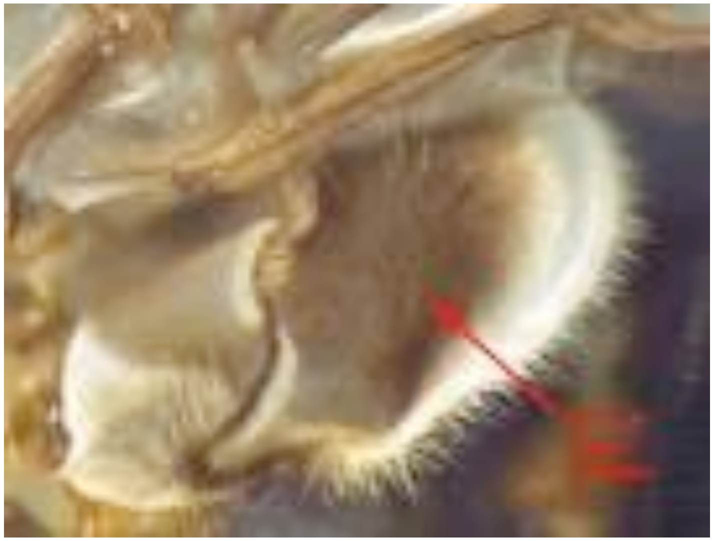
Cyclorrhapha=Those flies that escape from the puparium by pushing off the circular cap. Larvae mostly saprophagous. Adults lack the muscle plaques.



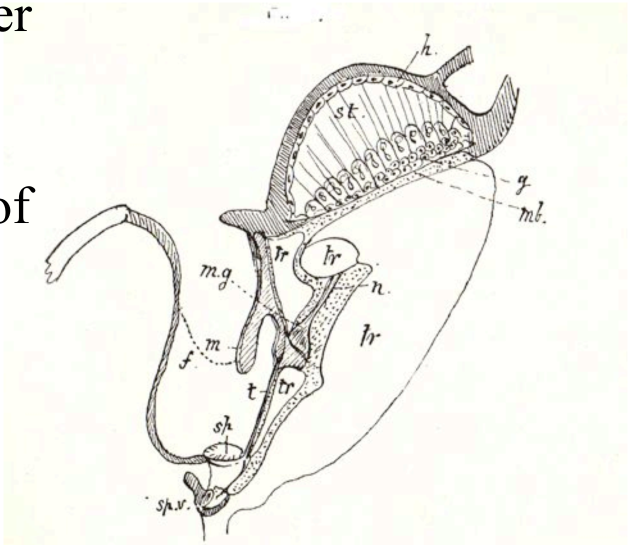
Schizophora= main trait is presence of the ptilinum

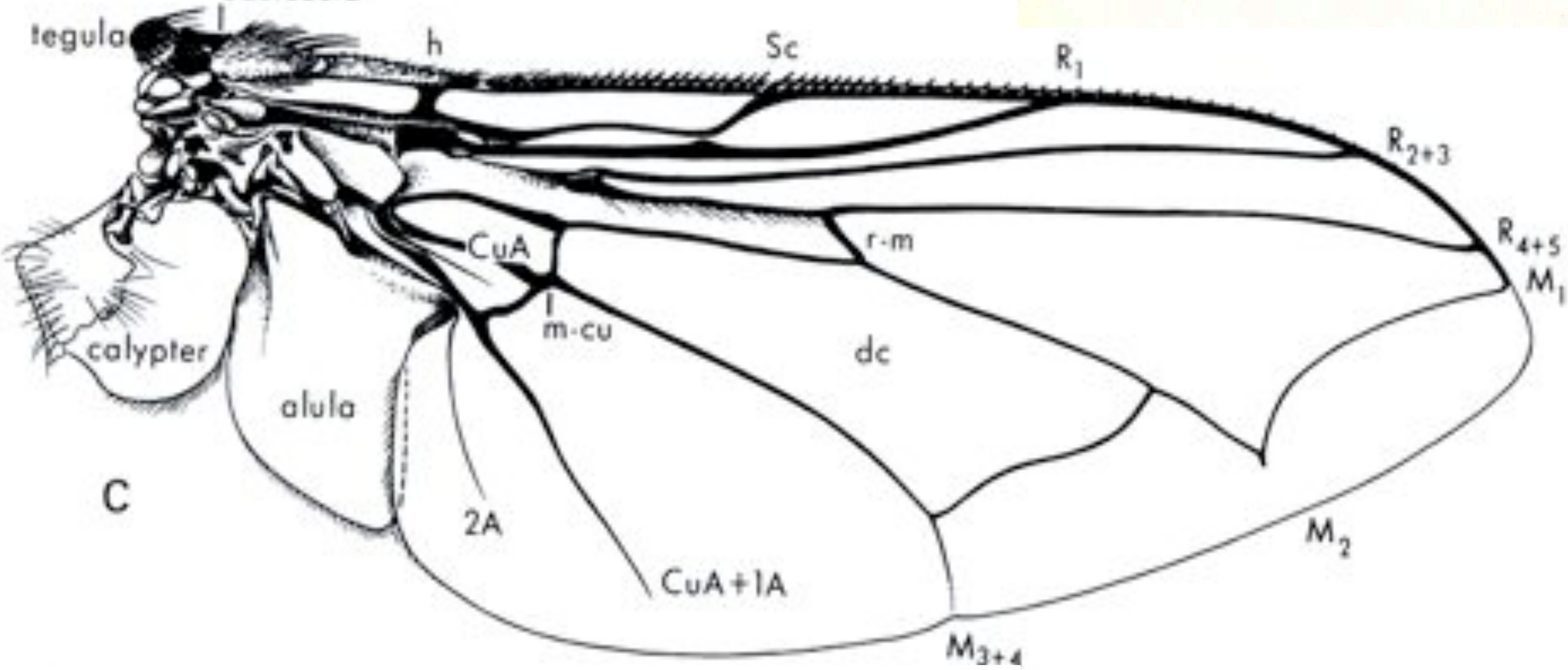
Use ptilinum

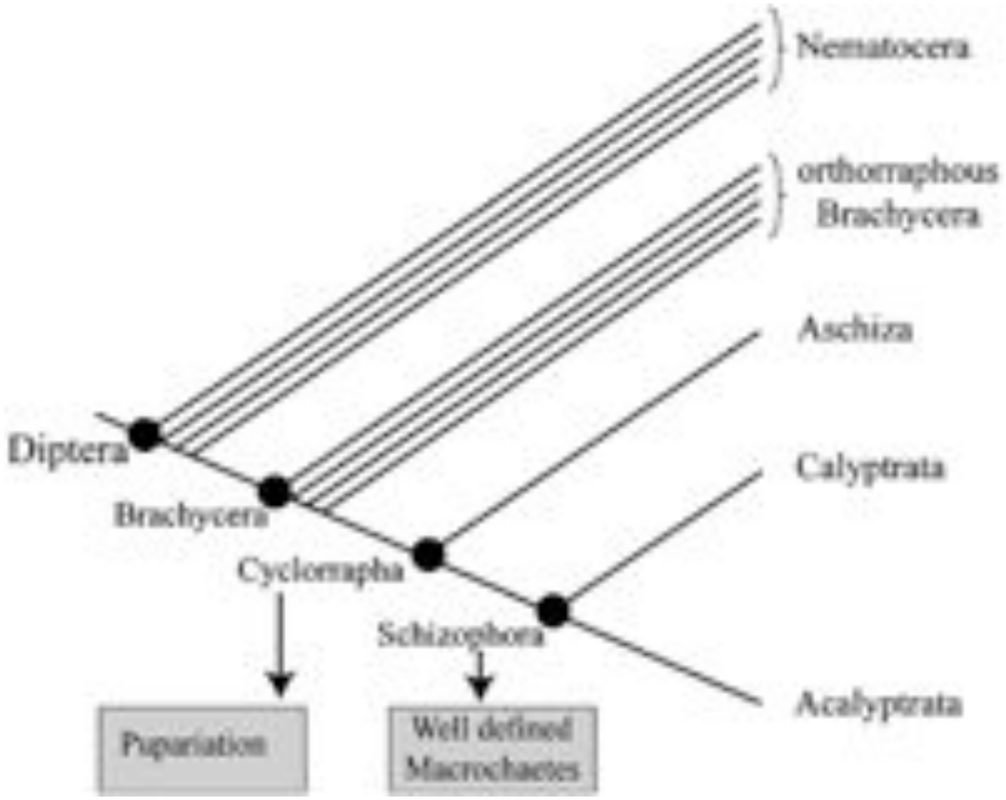
Calyptrates=possess a calypter or extra membrane of the wing that is above the halteres.



Stoffolano suggests that in the calyptrates, the calypter serves as a parabolic reflector directing sound into the tympanic fissure of the adult. See photo to the right showing this from Lownes 1890 book.







Phylogeny of the Diptera. The tree represents the phylogenetic relationships between the major taxa of Diptera. The Nematocera and the orthorraphous Brachycera are probably polyphyletic. The names of monophyletic groups are shown at the point of their emergence (filled black circles). The origin of the evolutionary novelties discussed in the text are indicated (grey boxes).

Heredity (2006) **97,** 148–156.

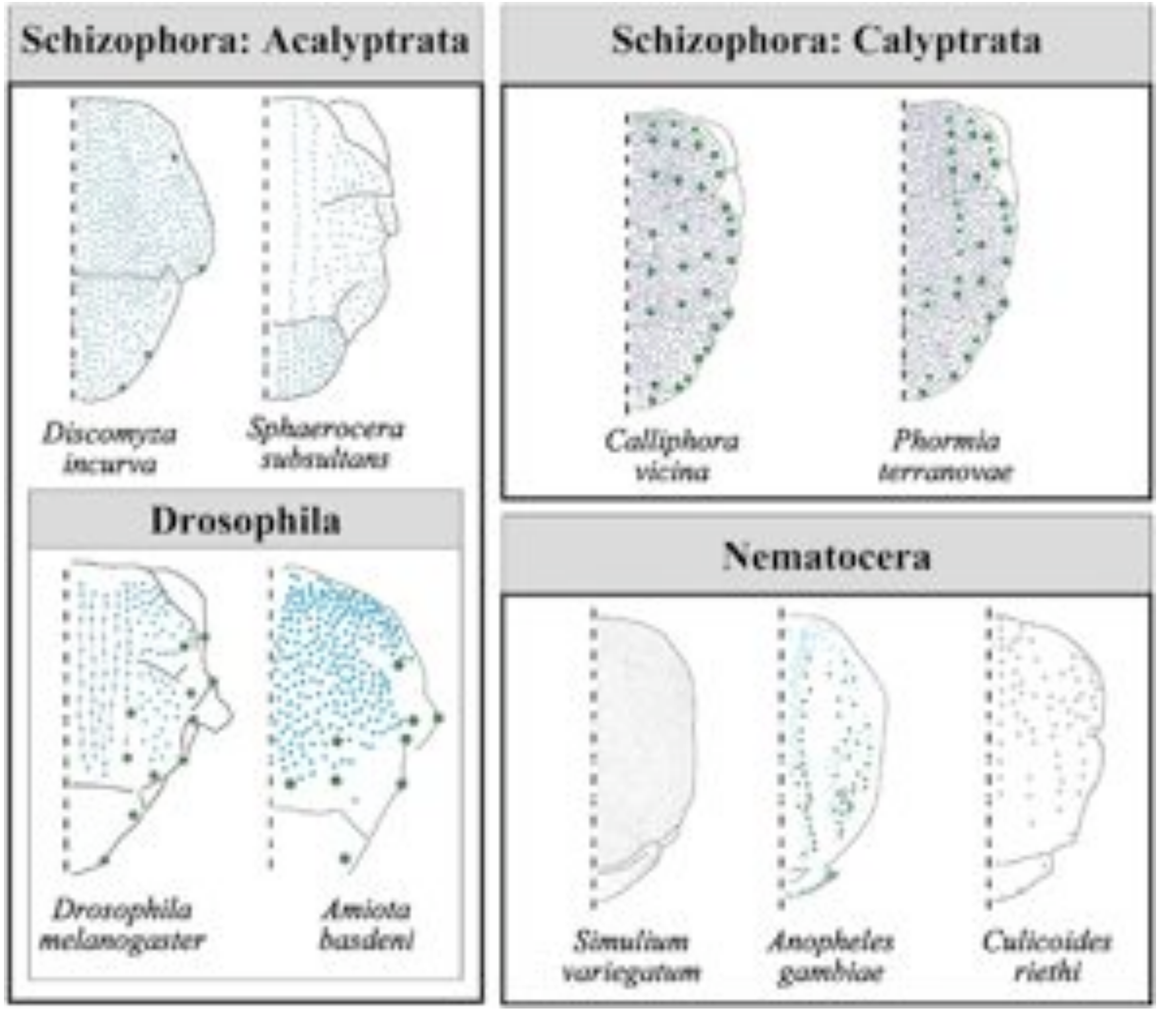
The origin and evolution of stereotyped patterns of macrochaetes on the nota of cyclorrhaphous Diptera

P Simpson[1] and S Marcellini

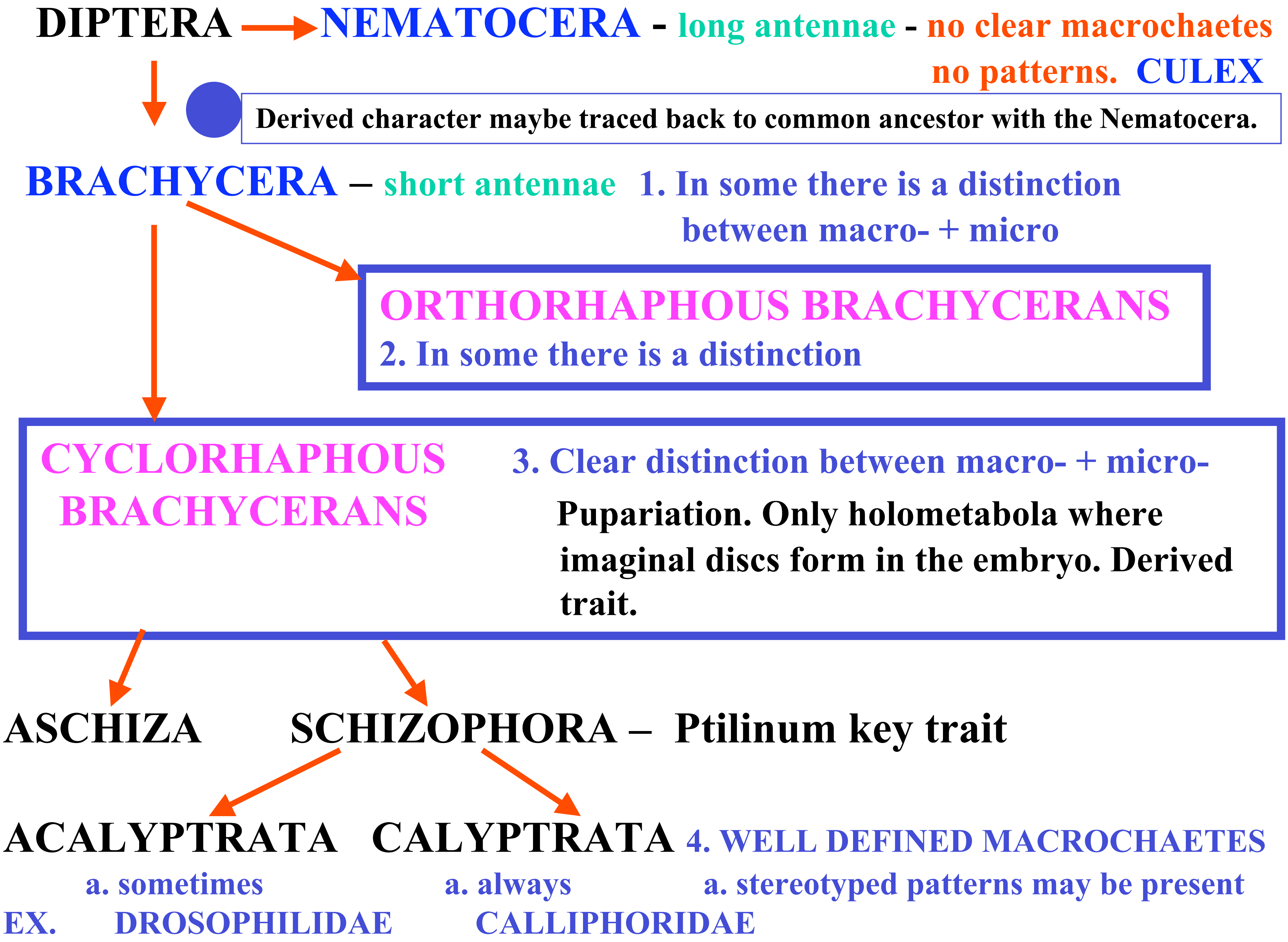
Two types of bristles

1. Microchaetes
    a. Precursors of are ‘Born’ during pupal period
    b. Closely spaced
    c. No defined function yet known
    d. Variable in number and function and no stereotyped patterns
    e. Short and thin

2. Macrochaetes-
    a. Precursors of are ‘Born’ early in larval development
    b. Not closely spaced
    c. Mechanoreceptors (directional sensitivity)
    d. Arranged in stereotyped way and set projection pattern into the thoracic ganglion
    e. Long, thick and stout



Schematic drawings of the thorax of species belonging to different groups of Diptera. Large green dots represent the macrochaetes and small blue dots the microchaetes. Species belonging to the Schizophora (see Figure 2) frequently bear stereotyped arrangements of macrochaetes. Of those mentioned in the text, *D. melanogaster* and *Ceratitis capitata* belong to the Acalyptrata, whereas *Calliphora vicina* and *Phormia terranovae* belong to the Calyptrata. All of these species have stereotyped bristle patterns. Nematoceran flies, in contrast, generally bear variable numbers of bristles rarely arranged into patterns. There are no clear macrochaetes in many members of this taxa (grey dots). Species of Nematocera mentioned in the text are *Anopheles gambiae, Culex pipiens, Clunio marinus, Toxorhynchites utilus, Chironomus thummi, Aedes aegypti* and *Chaoborus critillinus.* None of these have macrochaetes nor stereotyped bristle patterns.



DIPTERA → **NEMATOCERA** - long antennae - no clear macrochaetes no patterns. **CULEX**

● Derived character maybe traced back to common ancestor with the Nematocera.

BRACHYCERA – short antennae 1. In some there is a distinction between macro- + micro

ORTHORHAPHOUS BRACHYCERANS

2. In some there is a distinction

CYCLORHAPHOUS BRACHYCERANS

3. Clear distinction between macro- + micro-

Pupariation. Only holometabola where imaginal discs form in the embryo. Derived trait.

ASCHIZA

SCHIZOPHORA – Ptilinum key trait

ACALYPTRATA

a. sometimes

CALYPTRATA

a. always

4. WELL DEFINED MACROCHAETES

a. stereotyped patterns may be present

EX. DROSOPHILIDAE CALLIPHORIDAE

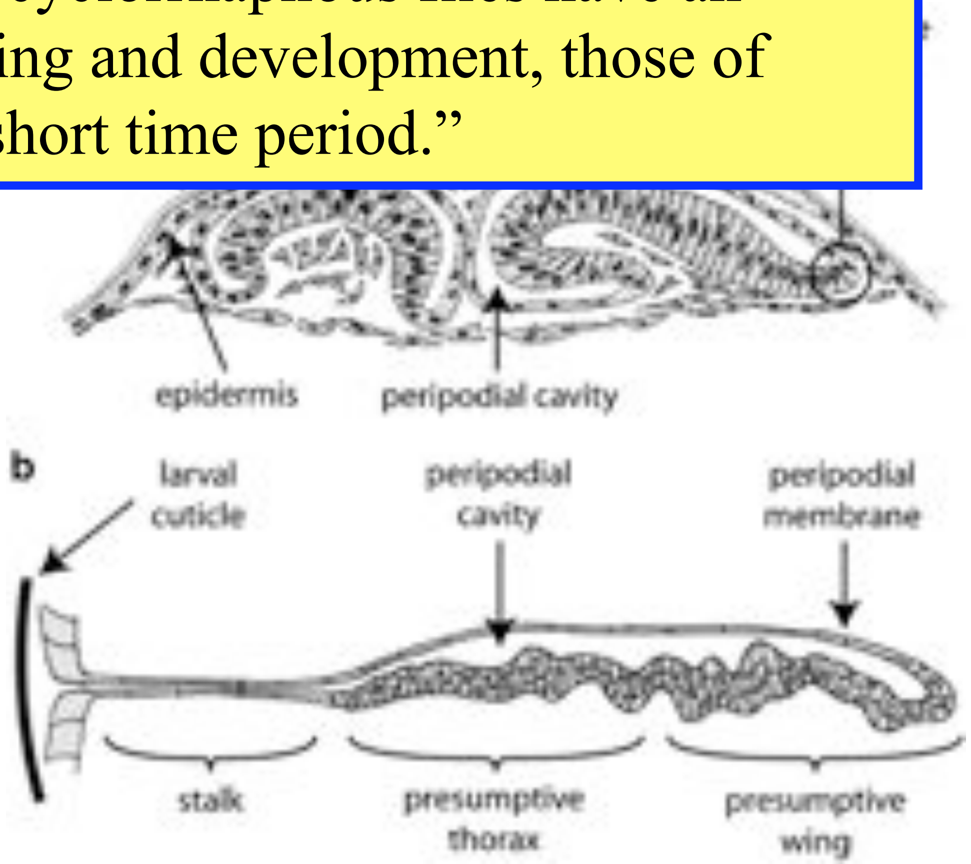
a. The imaginal discs in basal dipteran species such as *A. gambiae* (Nematocera), "…the future appendages are present as pouches budding from the larval epidermis. The future notum develops from a group of cells at the border between the larval and wing bug epithelia."

b. "In cyclorraphous Brachycera, as shown here for *D. melanogaster*, the developing imaginal discs are embedded well inside the larval body and remain connected to the larval epithelium through long thin stalks. The thorax and the wing both originate from the imaginal disc."

Conclusion here: Imaginal discs of cyclorrhaphous flies have an extended period of time for patterning and development, those of Nematocera develop over a rather short time period."

whole larval period. This means they have different exposure to hormones, etc., than the other dipterans.

2. "Appendages that are free of the body wall and develop during early larval stages represents a derived condition.
3. In the Nematocera "…imaginal discs only form at late larval stages (4th larval instar)."
4. Appendages in Nematocera are fastened down to the cuticle, unlike the Cyclorrhapha.

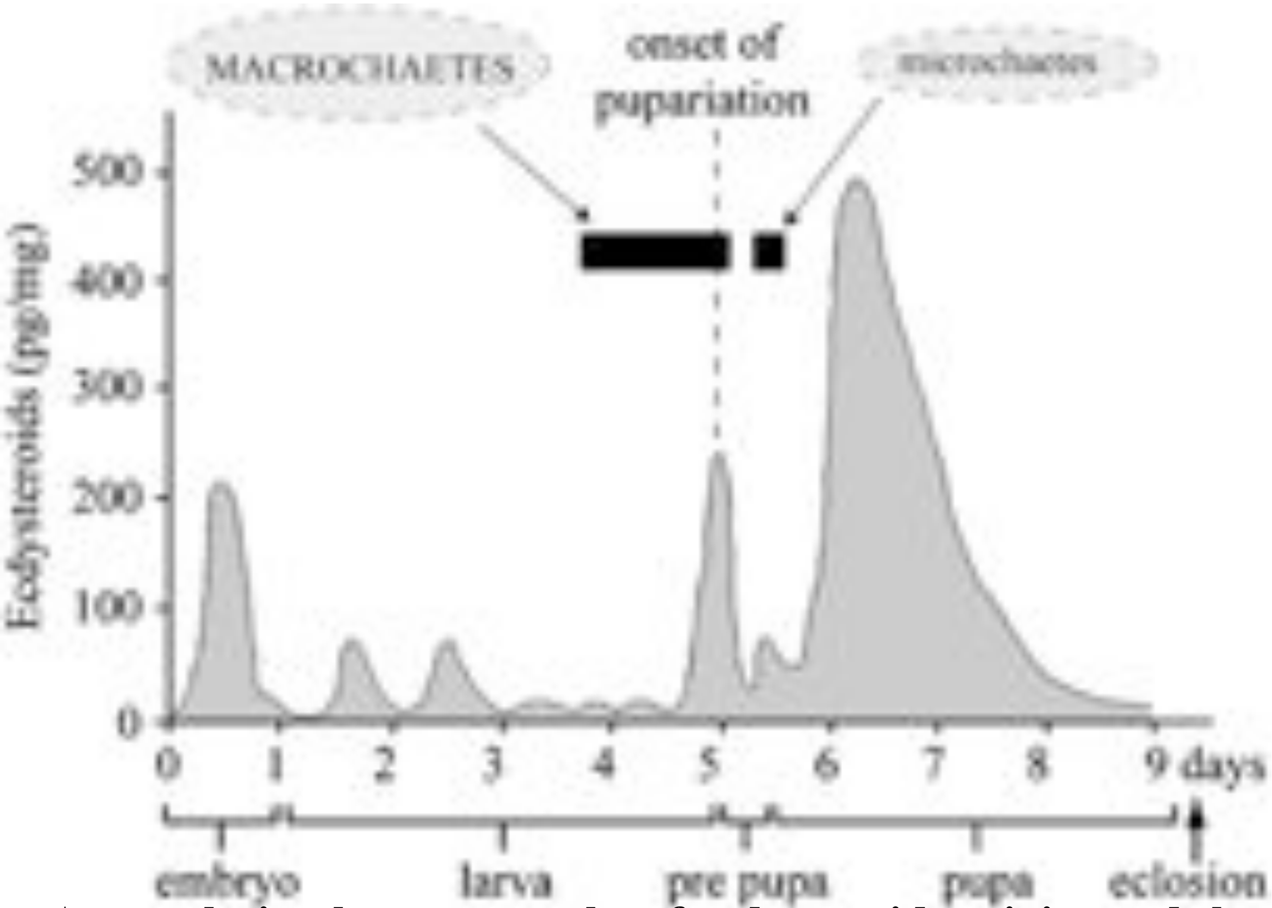


HETEROCHRONIC SHIFT IN PRONEURAL GENE EXPRESSION IN THE DIPTERA

"In biology, **heterochrony** is defined as a developmental change in the timing of events, leading to changes in size and shape. There are two main components, namely (i) the onset and offset of a particular process, and (ii) the rate at which the process operates. A developmental process in one species can only be described as heterochronic in relation to the same process in another species, considered the basal or ancestral state, which operates with different onset and/or offset times, and/or at different rates. The concept was first introduced by Haeckel in 1875[1].

Heterochronies are easily identifiable when comparing phylogenetically close species, for example a group of different bird species whose legs differ in their average length."

HERE, HOWEVER, WE ARE LOOKING AT THE TRAIT OF BRISTLE SIZE AND PATTERN IN THE DIPTERA.



A correlation between peaks of ecdysteroid activity and the formation of macrochaete precursors. The graph shows the pulses of 20E experienced by *D. melanogaster* during larval and pupal life. Adapted from (Riddiford, 1993) and (Warren *et al*, 2006). A small pulse during the third and last larval instar causes wandering of the larva and glue synthesis. Pupariation is initiated at five days of development during a peak of 20E (dotted line). The temporal windows during which macrochaete or microchaete precursors are specified are shown as black rectangles. Note that macrochaete precursors form before, and microchaete precursors after, the 20E pulse corresponding to pupariation.

PRONEURAL GENES *ACHAETA* (*AC*) AND *SCUTE* (*SC*)

encode

TRANSCRIPTION FACTORS OF THE BASIC-HELIX-LOOP-HELIX FAMILY

and

TOGETHER WITH DAUGHTERLESS

HOW COULD SUCH A HETEROCHRONIC SHIFT RESULT IN TWO DIFFERENT TYPES OF BRISTLES?

No. of separate phases of *ac-sc* expression → 2 for Brachycera <u>Calliphora</u> 1 for Nematocera **<u>Culex</u>**

Excess of *scute* gene in <u>Drosophila</u> before puparium formation gives additional macrochaetes but if after puparium formation only additional microchaetes

Thus, a shift in timing relative to what?

Could it be additional pulses of 20-H ecdysone?

<u>3 peaks of 20-hydroxyecdysone during larval stage</u>

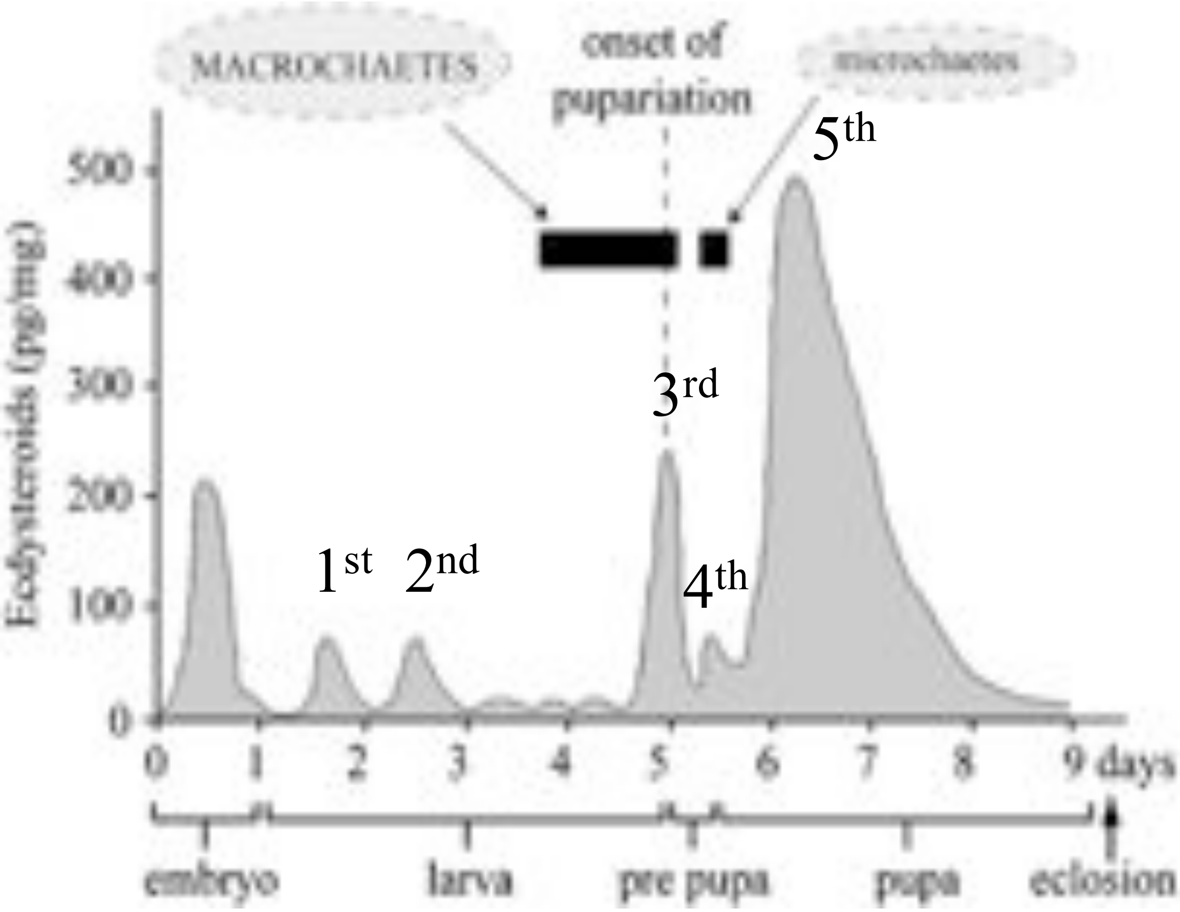
1st peak commits to pupariation

2nd peak initiates wandering of larva seeking pupation site

3rd peak correlates with pupariation

4th Causes head eversion and pupal cuticle deposition

5th Adult development

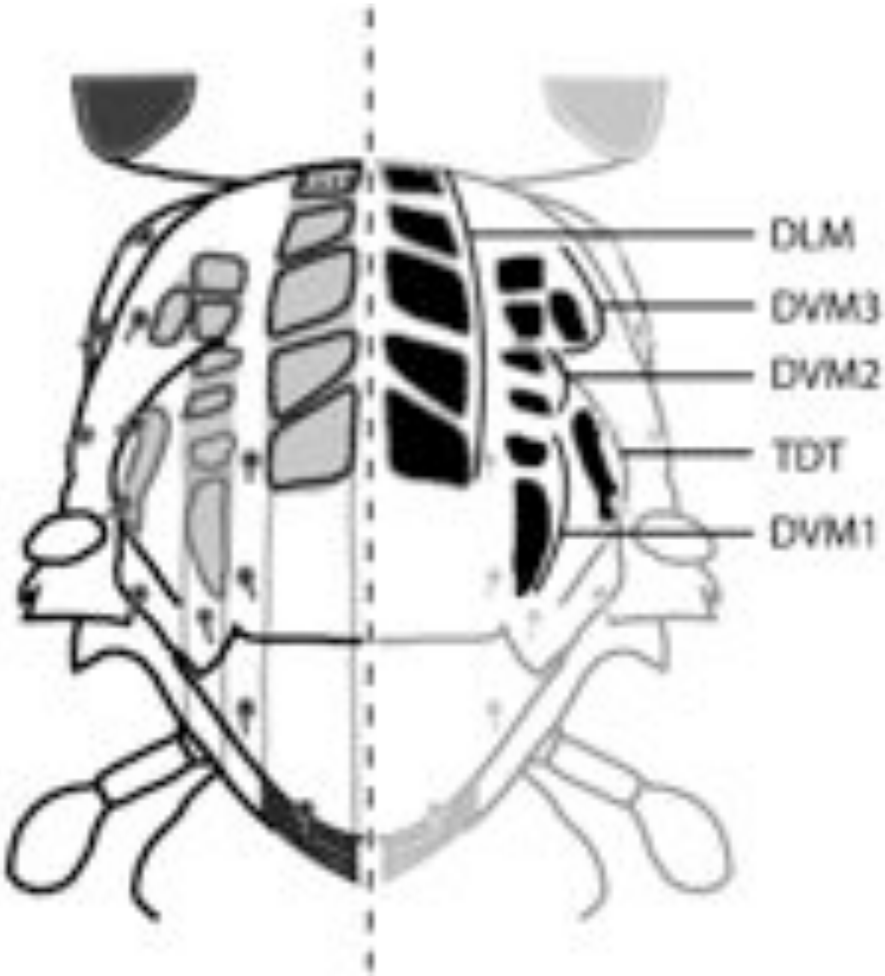


From what you know about muscle attachment and hypodermal cell fate, what can you say about where these bristles cannot locate or develop on the thorax?

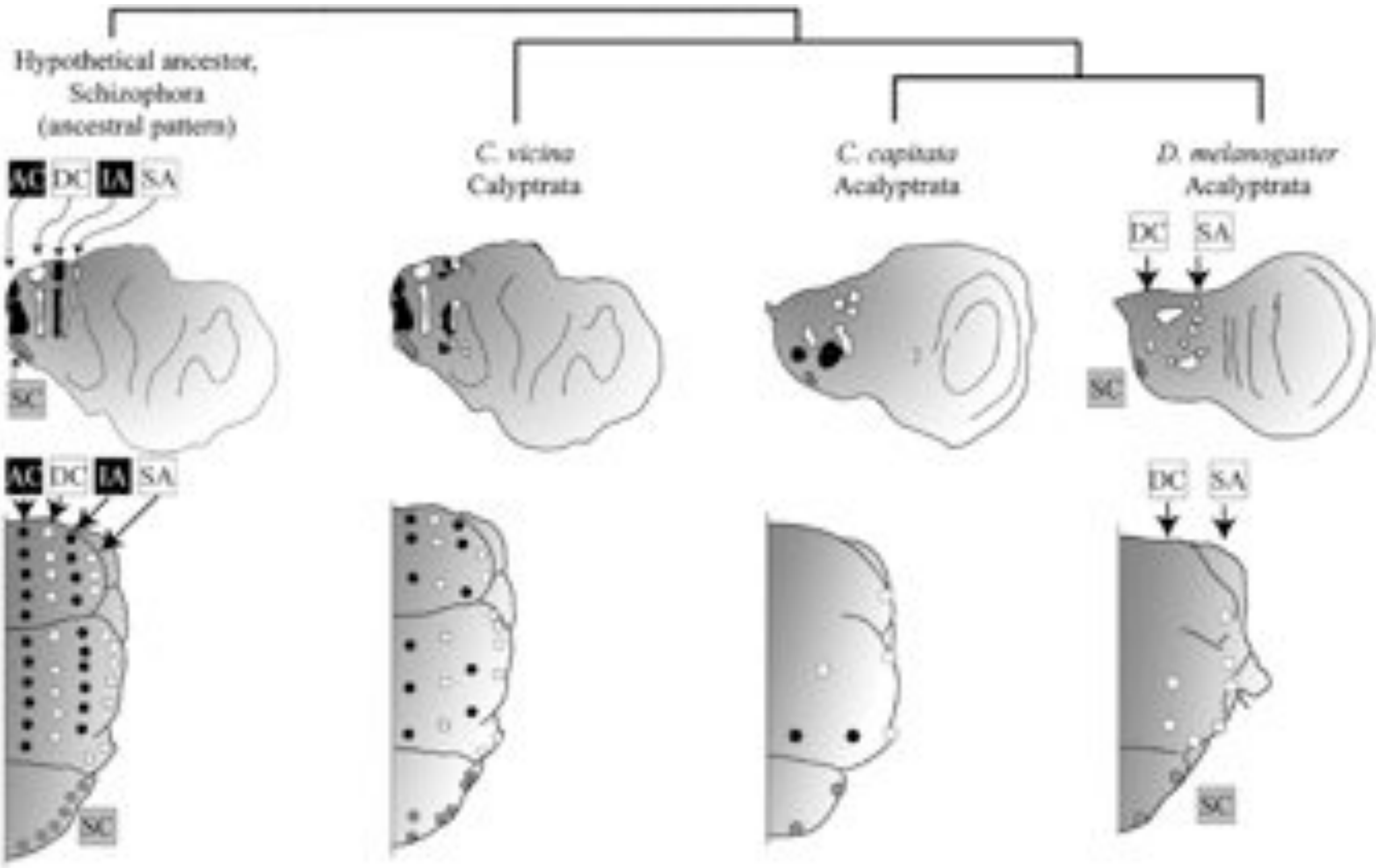
"…the additional bristles resulting from selection are not located over the sites of attachment of the flight muscles."

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

Remember the plaques story in the early dipterans. Here the hypodermal cells were specialized for tendon attachment of muscles and did not develop into cells that could also produce setae above them. Consquently, they produced a smooth cuticle.



The muscle attachment sites on the thorax of Diptera. The indirect flight muscles of Diptera attach to tendons whose precursors arise in the same imaginal epithelium as the bristle precursors, shown for *Drosophila* on the left. Note that the macrochaetes form between the muscle attachment sites (small circles). On the right, the muscle attachment sites are named and shown in black. Abbreviations: DLM, dorso-longitudinal; DVM, dorso-ventral; TDT, trochanter depressor. Adapted from Levine and Hughes (1973).



Proneural clusters may be derived from stripes of *sc* expression. Pistillo *et al* (2002) suggested that the proneural genes were expressed in an pattern of four longitudinal rows on the scutum of the ancestor leading to the Cyclorrapha (top left). These rows, and the bristles to which they give rise in the adult (bottom left) are named and represented with alternate black and white colour code. It is proposed that in the lineage leading to the Acalyptrata, different rows were entirely or partially lost, which correlates with a proneural gene expression pattern of reduced proneural clusters. As a result these flies have fewer bristles, but frequently in stereotyped arrangements on the notum. Abbreviations: AC, acrostichal; DC, dorsocentral; IA, intraalar; SA, supraalar; SC, scutellar. Adapted from Pistillo *et al* (2002).

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.

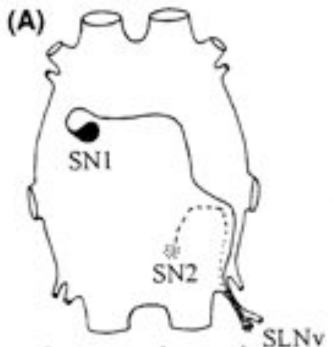
The overriding message in considering all of these adaptations is that no general consistent, morphological, physiological, or biochemical adaptations have been detected among all hematophagous lineages. However, the arthropods when faced with a common set of problems associated with gaining access to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

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

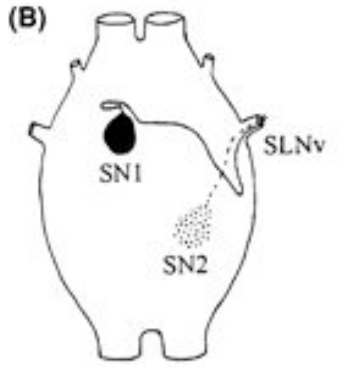
Ward C. Wheeler, Michael Whiting, Quentin D. Wheeler and James M.Carpenter

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*

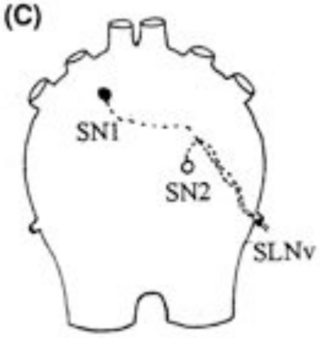
Ali, D.W. and D. C. Darling. 1998. Neuroanatomy and neurochemistry: implications for the phylogeny of the lower Neoptera. Can. J. Zool. 76: 1623-1633.



Locusta migratoria



Carausius morosus

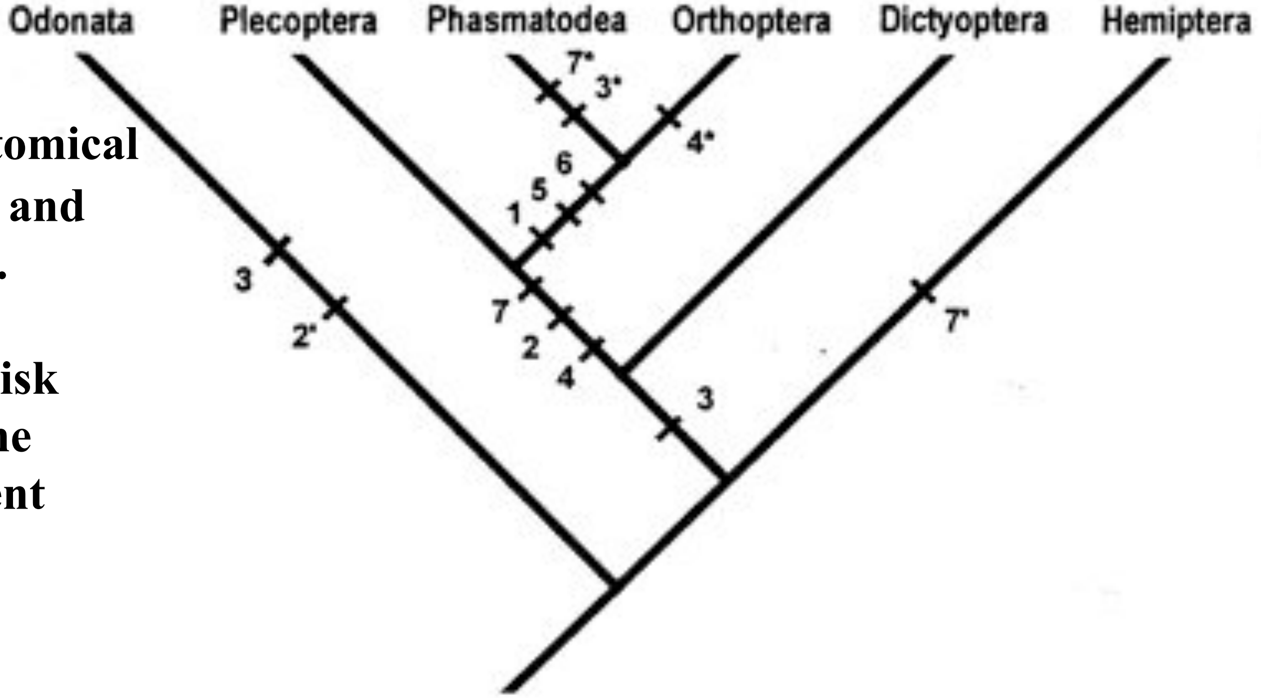


Periplaneta americana

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



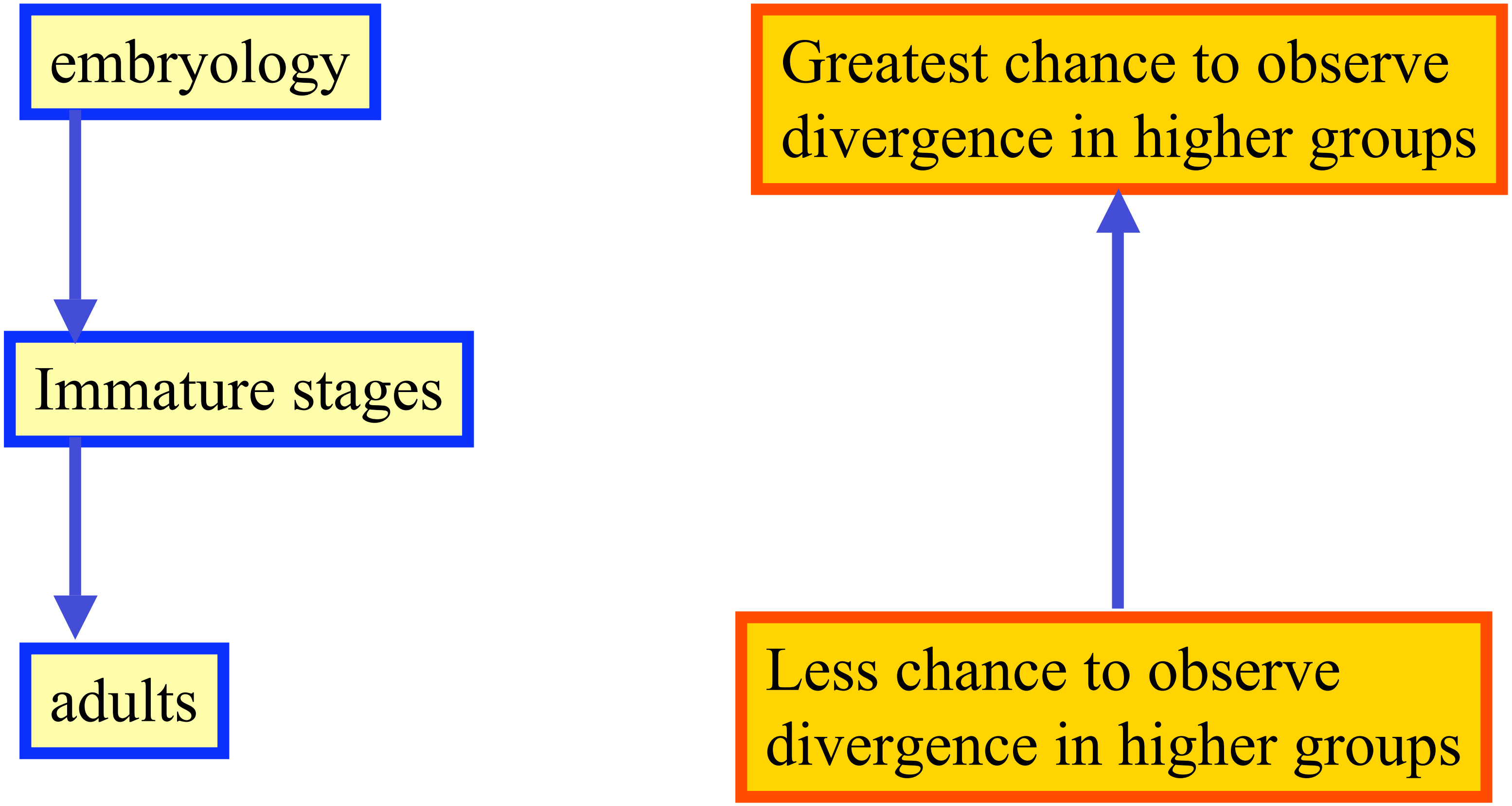
Data matrix for the neuroanatomical and neurochemical characters and most parsimonious cladogram. Shared derived characters are indicated by shading. An asterisk indicates a reversal and a prime symbol indicates an independent derived state.

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

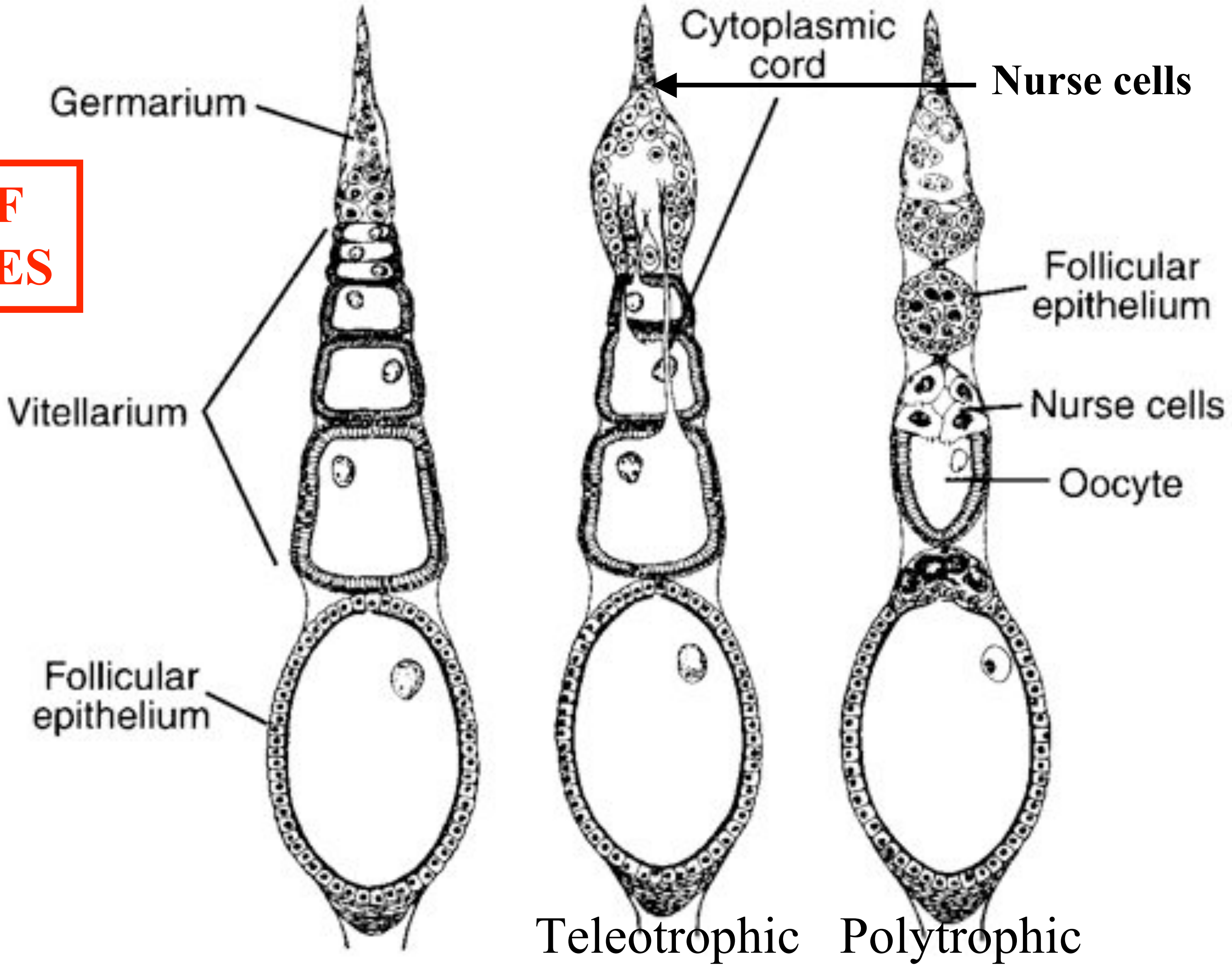
Greatest chance to observe divergence in higher groups

Less chance to observe divergence in higher groups

Gene sequencing
Genomics
Proteonomics

REPRODUCTIVE SYSTEM and the ovarioles

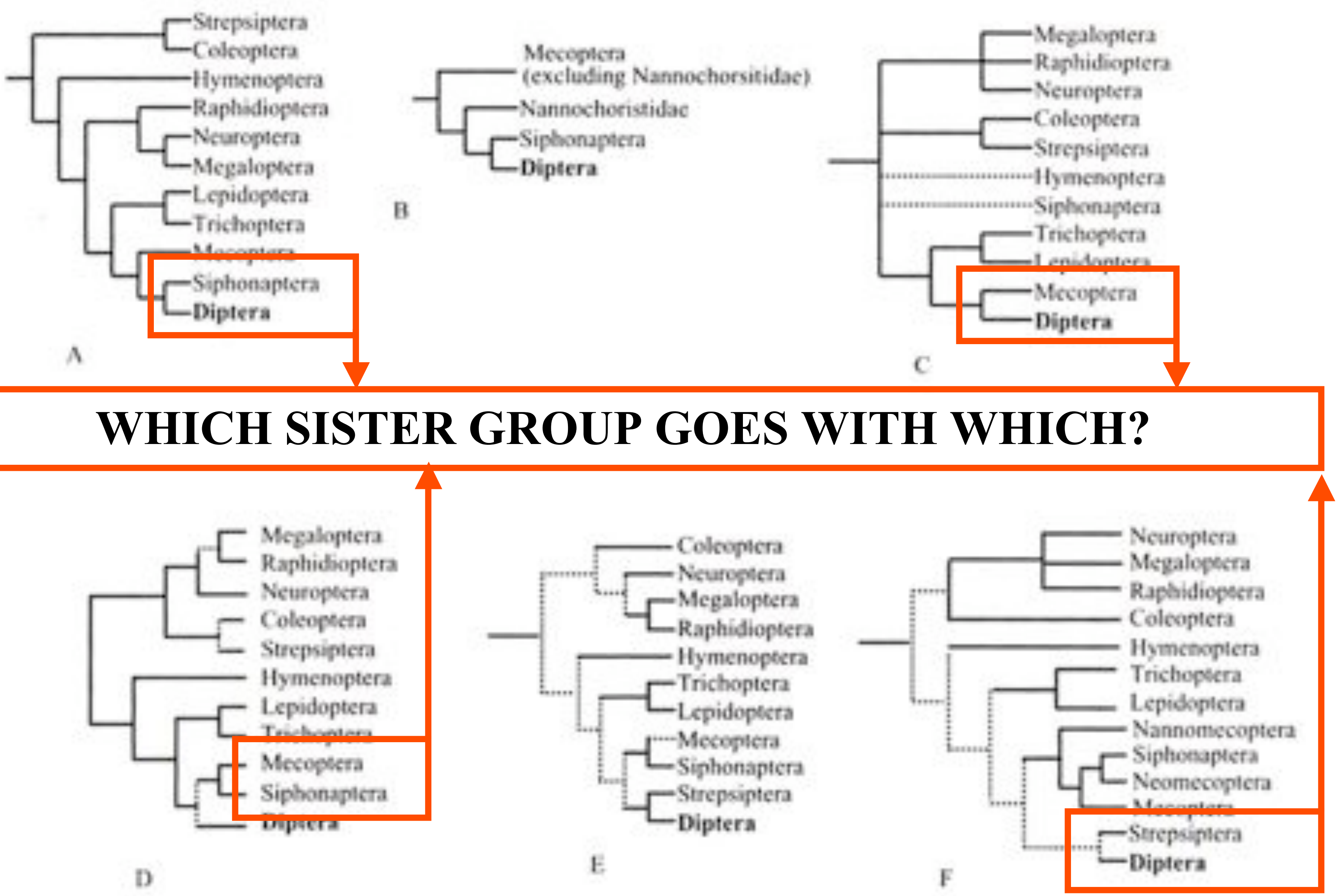
TYPES OF OVARIOLES



Teleotrophic Polytrophic

Panoistic
(no nurse cells)

Meroistic
(have nurse cells)



WHICH SISTER GROUP GOES WITH WHICH?

FIGURE 1.1. Previous phylogenetic hypotheses for the placement of Diptera among the holometabolous insect orders. (A) Boudreaux (1979), based on morphology; (B) Wood and Borkent (1989), based on morphology; (C) Hennig (1981), based on morphology; (D) Kristensen (1991), based on morphology; (E) Whiting et al. (1997), based on morphology and DNA; (F) summary tree, based on current molecular and morphological data. Dashed lines represent relationships that are considered poorly supported.

WHICH ORDER DO THESE INSECTS BELONG TO AND ARE THEY RELATED?

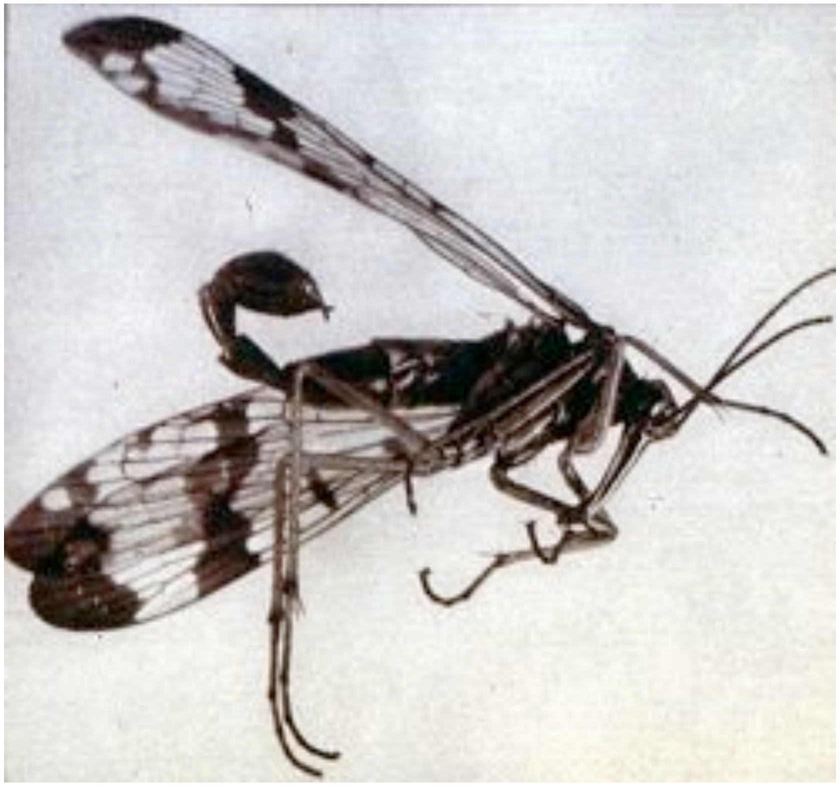
MECOPTERA (Boreidae)

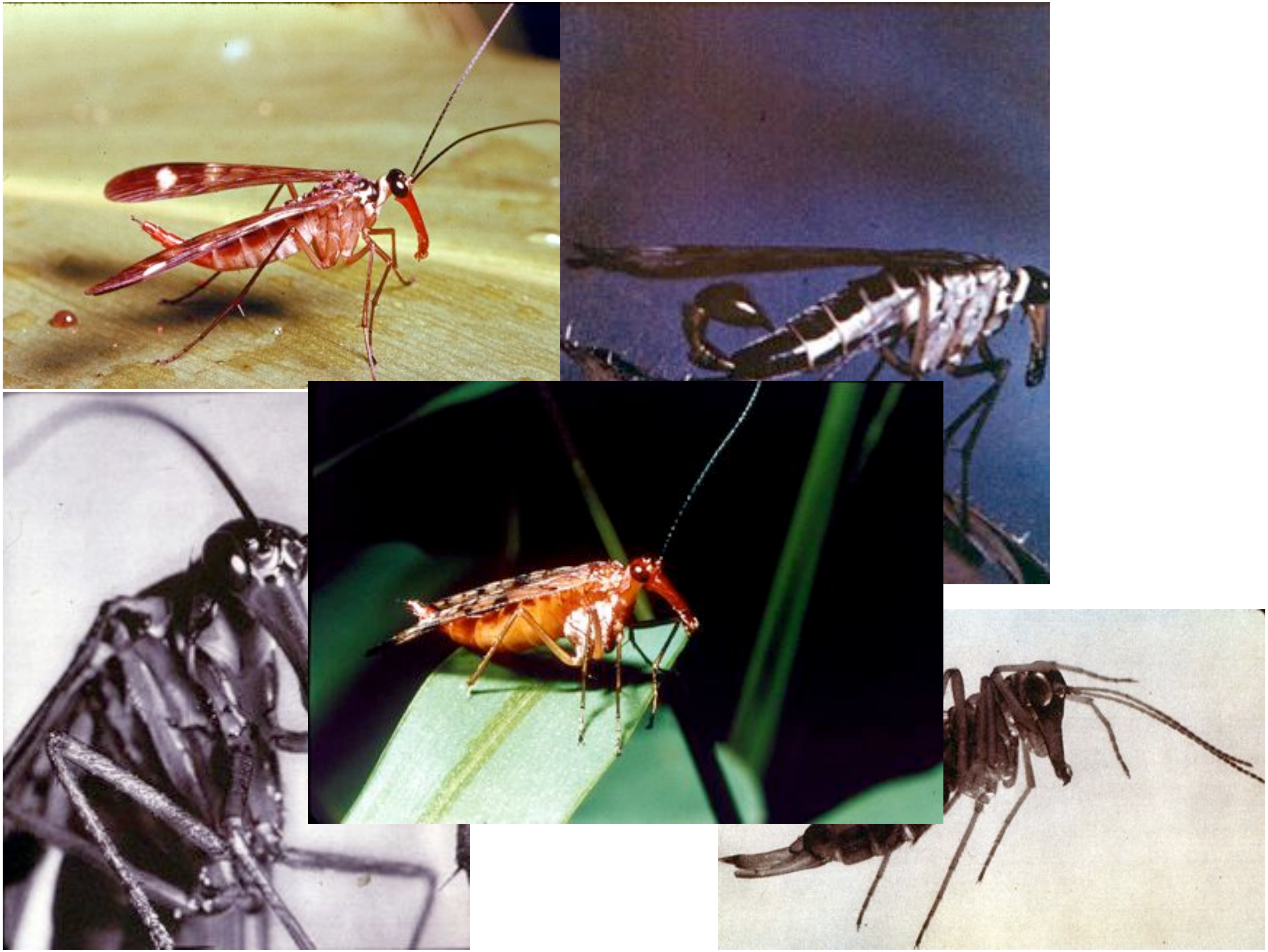
SIPHONAPTERA

Mecoptera-scorpionflies

KEY CHARACTERISTICS:

1. Males have scorpion-like abdomen
2. Elongated rostrum with mouthparts at the tip
3. Wings usually mottled





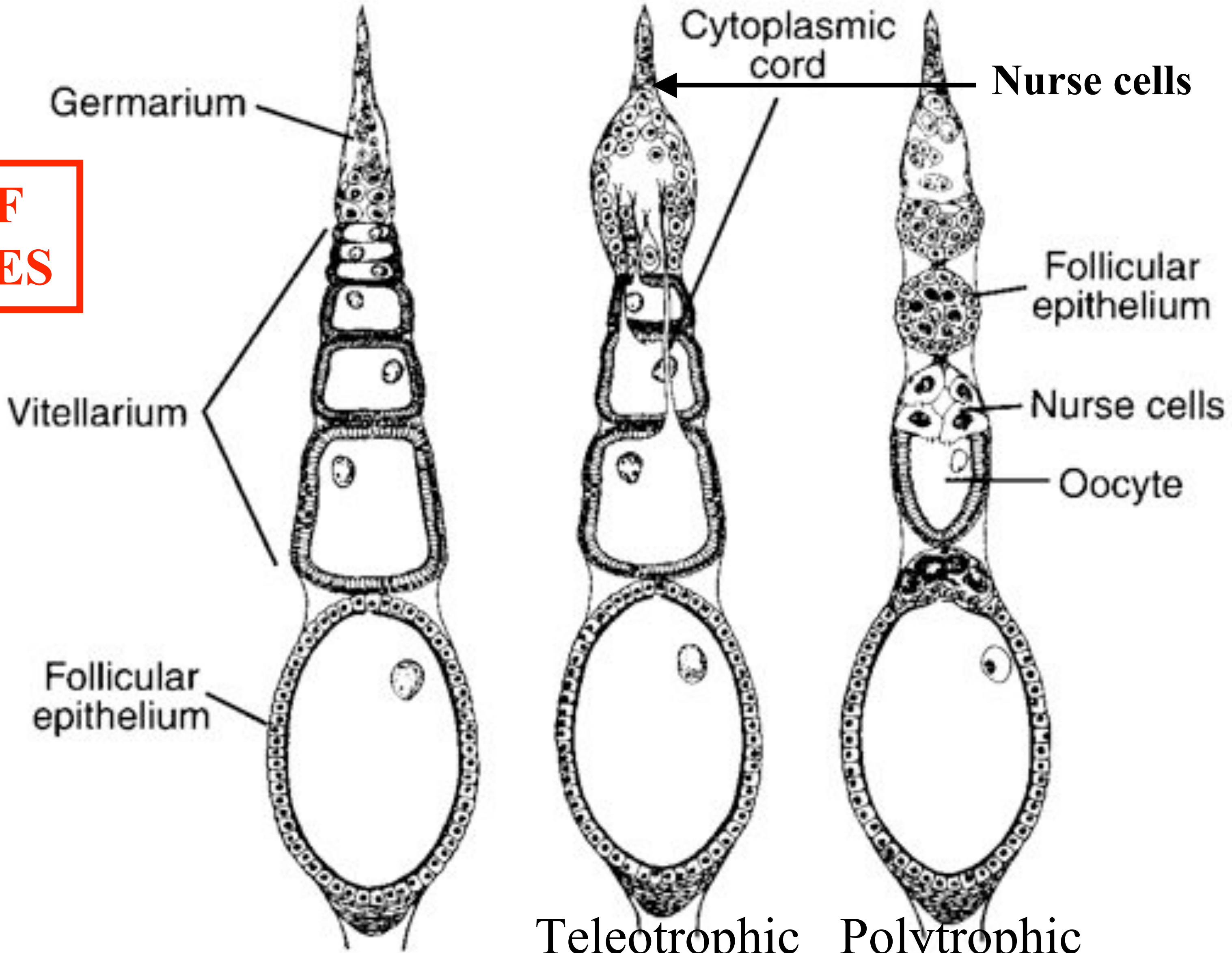
Siphonaptera-fleas

- KEY CHARACTERISTICS

1. Secondarily wingless
2. Piercing sucking mouthparts and feed on blood of mammals
3. Hindlegs modified for jumping
4. Are ectoparasites of mammals
5. Larvae live off the host and look like fly larvae
6. Major vector of disease causing agents of the Bubonic plague or Sylvatic plague

REPRODUCTIVE SYSTEM and the ovarioles

TYPES OF OVARIOLES



Nurse cells

Teleotrophic Polytrophic

Panoistic

(no nurse cells)

Meroistic

(have nurse cells)

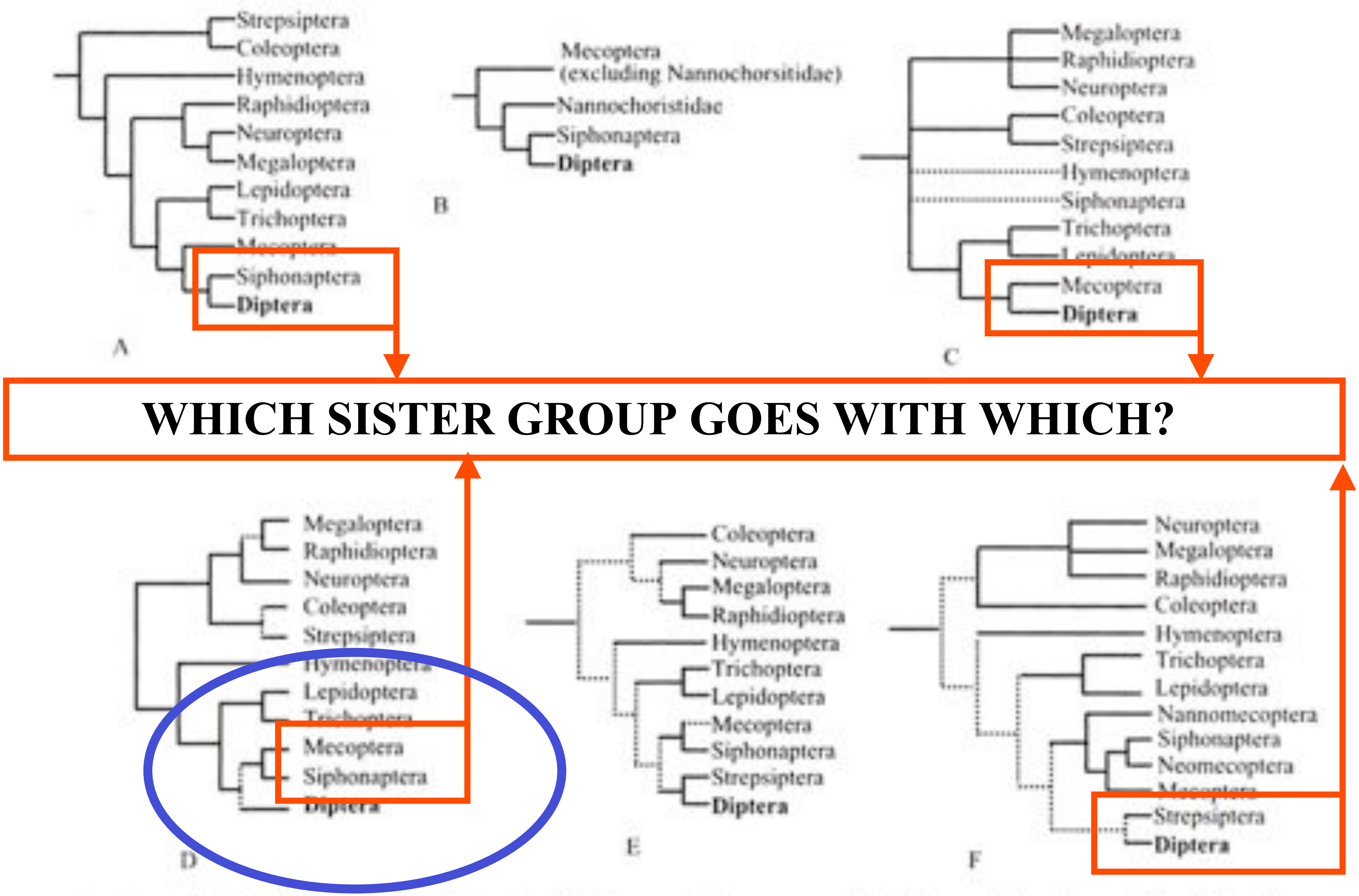
Evidence for putting fleas (Siphonaptera) as a sister group to the Boreidae and within the Mecoptera.

1. **Unusual proventricular spines in both are morphologically similar**
2. **Both have eyes in a skeletal socket**
3. **Both have multiple sex chromosomes**

MOST CONVINCING EVIDENCE COMES FROM OVARIOLES

4. **Boreid ovarioles differ from those of other mecopterans, which are polytrophic-meroistic and have nurse cells. Boreid ovarioles lack nurse cells as do those of the Siphonaptera, which are panoistic.**
    - **a. Secondary loss of nurse cells**
    - **b. Presence of accumulations of membrane-free, clathrinlike cages**

Bilinski, S., J. Bünnig, and B. Simiczyjew. 1998. The ovaries of Mecoptera: Basic similarities and one exception to the rule. Folia Histochem. Cytobiol. 36: 189-195.



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CONCLUSION FOR THE PHYSIOLOGY/SYSTEMATIC SECTION

1. **Morphology and the character states available are influenced by how the various systems interact to produce the phenotype.**
2. **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 organisms.**
3. **New genes are not produced but it is the way they are organized and the different developmental pathways they become involved in that produces the effect or phenotype we see in an individual group.**
4. **Using various character states (i.e., nervous system or bristle arrangement and type) researchers are able to use molecular/genetic techniques to examine that trait and recreate its phylogenetic path. In most cases, the character state examine follows and coincides with the phylogeny already developed by systematists.**
5. **Using adult character states to look at phylogeny in higher groups, one is less apt to find divergence. However, one has a greater chance of observing divergence in a character state in higher groups by looking at characters in embryonic development.**

CONCLUSIONS FOR THE COURSE

1. **Physiology is the study of how different systems of the organism interact with one another based on differential gene expression**
2. **Structure compliments function**
3. **Even within the same group, structure can vary depending on the life style of the insect**
4. **Behavior is just an expression of the underlying physiological interactions of the various systems**
5. **Morphology used by systematists is just an expression of the underlying physiological interactions of various systems**
6. **Physiology and the systems of study are influenced by differential gene expression and the various pathways involved**
7. **The generalizations or examples used to support a physiological event or process are usually based on a limited study of insect groups but are taken from the study of a model system**
8. **Model systems, which are few, in insect physiology have laid the ground plan for what we know. Only by studying other insects, can we broaden our understanding of insect physiology.**

HIERARCHY OF SCIENCE AND MATH

1. **Theoretical math -**
2. **Applied math – statistics**
3. **Theoretical physics**
4. **Applied physics**
5. **Theoretical chemistry**
6. **Applied chemistry**
7. **Theoretical biology –**
8. **Applied biology**

Scientists can exist with little information about the subject area below them

YES

NO

His talk at Umass in May, 2007, provided some ideas to think about as young scientists

1. Collaborate and share ideas
2. Make your avocation your vocation
3. Don't get stuck with an experiment. Sometimes you must give up and try a new experiment
4. Don't throw out the 'junk' in an experiment, it may contain something important. Remember the work of Steve Tobe and JHIII.

Craig Cameron Mello (born October 18, 1960 in New Haven, Connecticut is one of the laureates of the 2006 Nobel Prize for Physiology or Medicine, along with Andrew Z. Fire, for the discovery of RNA interference. This research was conducted at the University of Massachusetts Medical School and published in 1998, where Mello is professor of Molecular Medicine