Arthropod Phylogeny: A Summary by John Pinto, 1997
(with a few modifications by DAR, 1999)

The field of arthropod relationships remains an exceptionally controversial one. In fact, it is becoming questionable whether we can profitably cover this topic in this course. An excellent summary of the problems in this field can be found in Budd (1996). One of the major problems is that with the incorporation of molecular data, the picture of relationships has actually become less clear than before. While morphological or molecular data taken alone can give us reasonable concepts of relationship, results from the two seem to be largely incompatible. It thus appears that either the morphological or the molecular data (or both?) are totally erroneous. Some are arguing for a "total evidence" approach (e.g. Wheeler *et al.* 1993) (using all data together), but this in itself remains quite controversial. In any case, what follows is largely weighted in favor of morphological data, with comments on the molecular input where appropriate.

Polyphyletic vs. Monophyletic Theories:

The groups included in the Arthropoda include the chelicerates (arachnids, etc.), trilobites (trilobites), crustaceans, and uniramians (= Atelocerata, and includes the insects and myriapods). A polyphyletic theory of the group entertained by some is that the 4 major arthropod groups do not share a common ancestor that was itself an arthropod; rather all 4 groups arose independently from different annelid or annelid-like ancestors and all "arthropod characters" of the major groups are homoplastic. Manton (1997, etc.) was a major proponent of this theory. She believed the mandibles of uniramians and crustaceans were so different that the groups couldn't be related. She noted that crustacean mandibles are multiarticulate appendages in which the biting and chewing surfaces are highly developed coxal endites, or gnathobases (gnathobasic jaw). Uniramian mandibles on the other hand are of a single (whole limb jaw). The absence of fossil organisms representing "missing lings" or intermediate forms between the arthropod groups was also used as evidence for this theory.

Yet others have noted that mandibles of both types are fundamentally similar in that they represent the appendages of the second postoral somite that simply possess modifications upon a basic structural type - ie. they are homologous. Crustacean mandibles retain the multiarticulate limb (in the form of a palp), whereas uniramians long ago lost all vestiges of this multiarticulate form. Both types, however, are easily derived from the same simple jointed appendage of third postacronal segment especially when considering the 550-million years independent history of the two lineages.

The proponents of a polyphyletic theory failed to do one thing: and that is to show that one or more of the four major arthropod lines is more closely related to some other group of non-arthropod organisms than it is to the other arthropods. No such evidence has ever been presented. Basically the polyphyletic school stresses the differences of the various taxa, without attempting to challenge the similarities which are hypothesized as synapomorphic for the groups. This theory is impressed by divergence but fails to consider "hypothetical ancestors;" instead it simply argues against extant forms serving as ancestors. Good criticism of the polyphyletic theory is provided by several authors (e.g. Weygoldt 1979, Kristensen, 1991).

General consensus is becoming that the Arthropoda is a monophyletic group. In any case, it is clear that most of the polyphyletic theory is based on weak phylogenetic reasoning and there is not persuasive reason not to consider the group as monophyletic. Yet we should keep in mind that within each of the 4 major arthropod clades, there are indeed numerous convergences. Given the great age and size of the groups, a high level of convergence is not surprising. Among them are probably:

a. Tracheae, which may have evolved independently at least 4 times (onychophorans, arachnids, terrestrial isopod crustaceans, tracheates [and possibly separately in myriapods and insects as well]).
b. Malphigian tubules probably evolved 3 times (tardigrades, insects, arachnids).
c. Loss of compound eyes has occurred independently in each line.

A recent study by Wheeler *et al.* 1993 is an important paper that puts another nail in the coffin of polyphyletic theory. The authors examine relationships using morphological characters and ribosomal and

Trilobitomorpha, Chelicerata, Crustacea, Uniramia

Fossil record of arthropods dates back to earliest Paleozoic. By that time all four subphyla were in existence and had already undergone substantial radiation. In other words, 4 principal clades had begun to diverge before the first arthropods were fossilized. Earliest trilobite, crustacean, and cheliceriform fossils date from Cambrian; myriapods appeared by at least the Silurian; hexapods (insects) by Devonian, and winged insects by Carboniferous. Thus paleontology has little to tell us about origins and relationships of the 4 groups.

Various hypotheses have been proposed for describing the relationships of these 4 groups. Much of the controversy revolves around 2 items: a) biramous limbs of trilobites and crustaceans homologous or not; b) mandibles of uniramians and crustaceans homolgous or not. Further problems revolve around what obviously must be considerable homoplasy in numerous structures (eg. air-breathing tracheae probably evolved independently 4 times; malpighian tubules occur in tardigrades, insects, and arachnids, buta are different in each; within each line at least some groups have undergone parallel loss of the lateral compound eyes). As indicated above, there is no reason not to consider mandibles of crustaceans and uniramians homologous. The question of biramy doesn't concern us here.

Trend is now to consider crustaceans and tracheates as sister groups (Mandibulata). Character analysis and fossil appearance suggests that the arthropods diverged probably in Precambrian into 2 lines: one lacking true 'jaws" (cheliceriformes and trilobites), the other with jaws (crustaceans, uniramians). Transition from aquatic crustacean-like ancestor to primitive aquatic uniramian may have taken place over 600 mya in early Paleozoic times. The oldest known uniramian fossils are marine myriapods from the Silurian. Terrestrial myriapods first appear in Devonian and represent some of the earliest known land animals. Myriapods developed aerial tracheal system and water conservation structures (malpighian tubules) on land. Loss of the compound eyes in myriapods probably took place after the origin of the first insects, since Devonian myriapods still possessed faceted eyes.

A 19 + 2 plan (19 true somites plus acron and telson) occurs in what many feel are the most primitive myriapods, as well as in some remipedes and in the malacostracan crustaceans. Some suggest that perhaps the 19 + 2 body plan might be ancestral to all living arthropod taxa. This implies that the highly multisegmented arthropods (e.g. chilopods, diplopods) are a derived condition.

Synapomorphies of Crustacea + Tracheata:
a. similar ommatidial structure in compound eye.
b. tripartite brain.
c. mandibles present as appendages of same postacronal head somite.
d. 2 pairs of maxillae present and associated with same postacronal head somites.
e. head appendages used for feeding.

Crustaceans distinguished from Uniramia by:
a. naulius larva
b. "gnathobasic" mandibles; and perhaps
c. presence of stalked compound eyes.
d. biramous second antennae
"Perhaps" because polarity of these characters remains somewhat controversial.

Synapomorphies of Tracheata:
a. anterior tentorial arms
b. absence of distinct tritocephalic head segment and associated second antennae.
c. absence of a pretarsal levator muscle.
d. loss of palp (telopodite) on mandible.
e. malpighian tubules (independently reduced in both groups).
f. 6 tracheae? (remains doubtful homology in myriapods, entognathous insects and ectognathous insects because of
       considerable diversity in the topography of spiracles in these three groups).

(Chelicerata (Crustacea (Myriapoda, Hexapoda))).

A paper by Boore *et al.* (1995) is one of the more recent challenges of this view. Using mitochondrial gene arrangement comparisons they argue for the following:

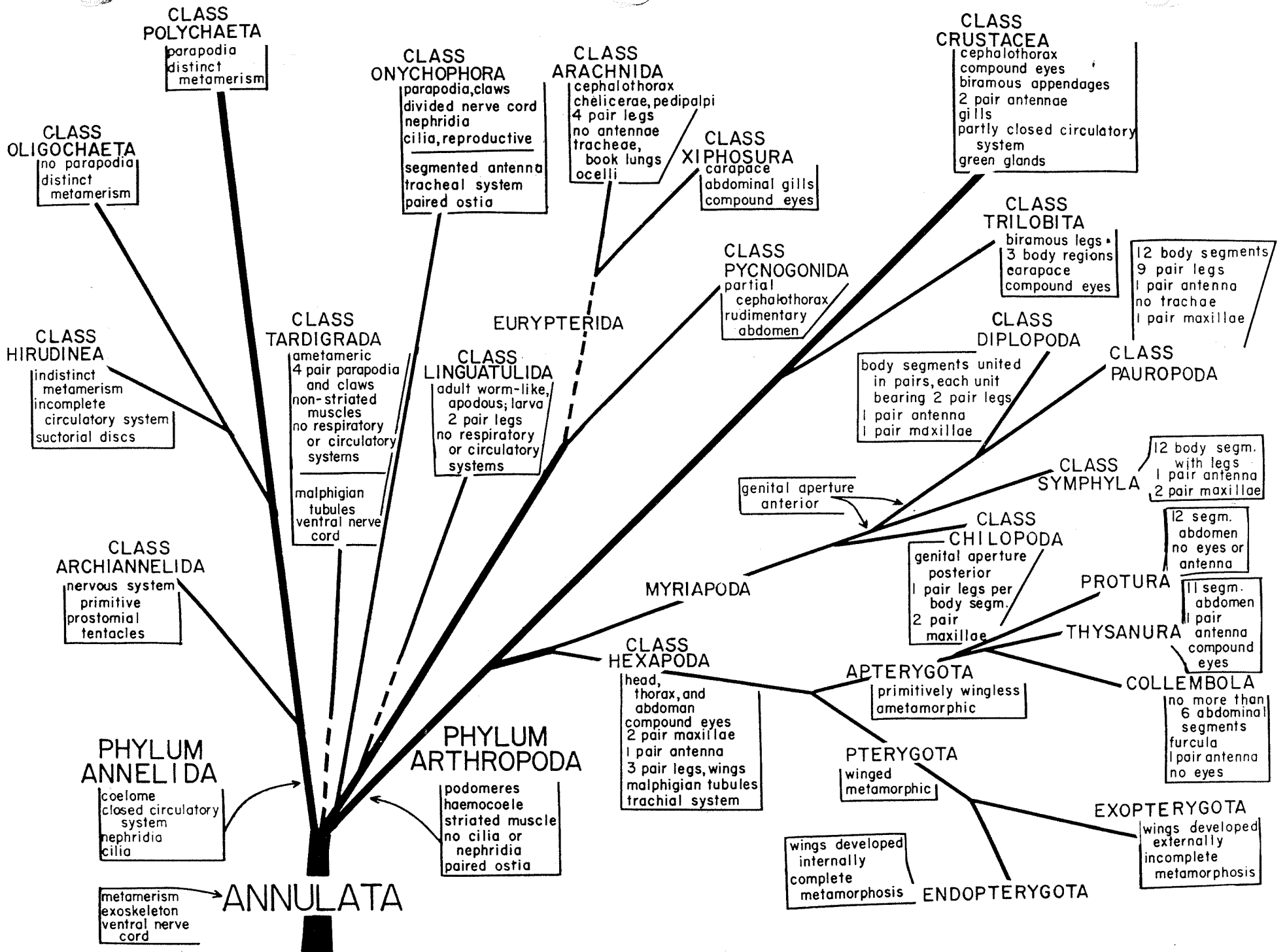((Chelicerata, Myriapoda) (Crustacea, Hexapoda)).

They would argue that the morphological similarities suggesting the first cladogram is based on convergences. The most important traits used for this scenario are (1) Malpighian tubules, (2) Tracheae, (3) One pair of antennae on the head instead of two as in Crustacea. They note that 1 and 2 are not restricted to the two tracheate groups but occur in other land-living arachnid taxa as well. Regarding the loss of the 2nd antennae, they argue that the ancestral function of these antennae is that of locomotion under water and of filter feeding. On land these functions are dispensable and their independent loss in myriapods and hexapods (and retention in the crustaceans) should not be surprising.

They also argue that actually certain morphological features argue for their hypothesis as well. For example, the structure of the compound eye is extremely similar in crustaceans and hexapods but considerably different in myriapod and chelicerate groups (in the few cases where they are retained). Also, the mandibles (which gives the name Mandibulata to the myriapod, crustacean, hexapod assemblage) are not necessarily homologous. They point out that in crustaceans and hexapods the mandibles are short, solid and gnathobasic, whereas in every major subgroup of Myriapoda there are examples of jointed mandibles.

A general criticism of the molecular data studies is that too few taxa have been examined thus far. For example, the work by Boore *et al.* (1995) includes only three myriapods, two chelicerates, two crustaceans, and three hexapods. These data also suffer from the inability to incorporate fossil groups such as trilobites, which are generally considered closest to the Chelicerata.

References:
Boore, J. L., T. Collins, D. Stanton, L. Daehler, & W. Brown. 1995. Deducing the pattern of arthropod phylogeny from mitochondrial DNA rearrangements. Nature 376:163-167.
Brusca, R. C. & C. J. Brusca. 1990. The Invertebrates. Sinauer Assoc., Sunderland, 922 pp.
Budd, G. E. 1996. Progress and problems in arthropod phylogeny. Trends in Ecol. & Evol. 11:356-358.
Stys, P. & J. Zrzavy. 1994. Phylogeny and classification of extant Arthropoda: Review of hypotheses and nomenclature. Eur. J. Entomol. 91:257-275.
Wheeler, W. C., P. Cartwright, & C. Hayashi. 1993. Arthropod phylogeny: A combined approch. Cladistics 9:1-39.

CLASS POLYCHAETA
parapodia
distinct metamerism

CLASS OLIGOCHAETA
no parapodia
distinct metamerism

CLASS ONYCHOPHORA
parapodia, claws
divided nerve cord
nephridia
cilia, reproductive

segmented antenna
tracheal system
paired ostia

CLASS ARACHNIDA
cephalothorax
chelicerae, pedipalpi
4 pair legs
no antennae
tracheae,
book lungs
ocelli

CLASS XIPHOSURA
carapace
abdominal gills
compound eyes

CLASS CRUSTACEA
cephalothorax
compound eyes
biramous appendages
2 pair antennae
gills
partly closed circulatory
system
green glands

CLASS TRILOBITA
biramous legs •
3 body regions
carapace
compound eyes

12 body segments
9 pair legs
I pair antenna
no trachae
I pair maxillae

CLASS HIRUDINEA
indistinct metamerism
incomplete circulatory system
suctorial discs

CLASS TARDIGRADA
ametameric
4 pair parapodia and claws
non-striated muscles
no respiratory or circulatory systems

malphigian tubules
ventral nerve cord

EURYPTERIDA

CLASS LINGUATULIDA
adult worm-like,
apodous; larva
2 pair legs
no respiratory or circulatory systems

CLASS PYCNOGONIDA
partial cephalothorax
rudimentary abdomen

CLASS DIPLOPODA
body segments united in pairs, each unit bearing 2 pair legs
I pair antenna
I pair maxillae

CLASS PAUROPODA

CLASS SYMPHYLA
12 body segm.
with legs
I pair antenna
2 pair maxillae

genital aperture anterior

CLASS CHILOPODA
genital aperture posterior
I pair legs per body segm.
2 pair maxillae

CLASS ARCHIANNELIDA
nervous system primitive
prostomial tentacles

MYRIAPODA

PROTURA
12 body segm.
abdomen
no eyes or antenna

THYSANURA
II segm.
abdomen
I pair antenna
compound eyes

COLLEMBOLA
no more than 6 abdominal segments
furcula
I pair antenna
no eyes

CLASS HEXAPODA
head, thorax, and abdoman
compound eyes
2 pair maxillae
I pair antenna
3 pair legs, wings
malphigian tubules
trachial system

APTERYGOTA
primitively wingless
ametamorphic

PHYLUM ANNELIDA
coelome
closed circulatory system
nephridia
cilia

PHYLUM ARTHROPODA
podomeres
haemocoele
striated muscle
no cilia or nephridia
paired ostia

PTERYGOTA
winged
metamorphic

EXOPTERYGOTA
wings developed externally
incomplete metamorphosis

wings developed internally
complete metamorphosis

ENDOPTERYGOTA

metamerism
exoskeleton
ventral nerve cord

ANNULATA

Labels on figure (a) and (b): compound eye, cephalon, pygidium, antenna, labrum, gnathobase, endopod, lamellae on outer ramus
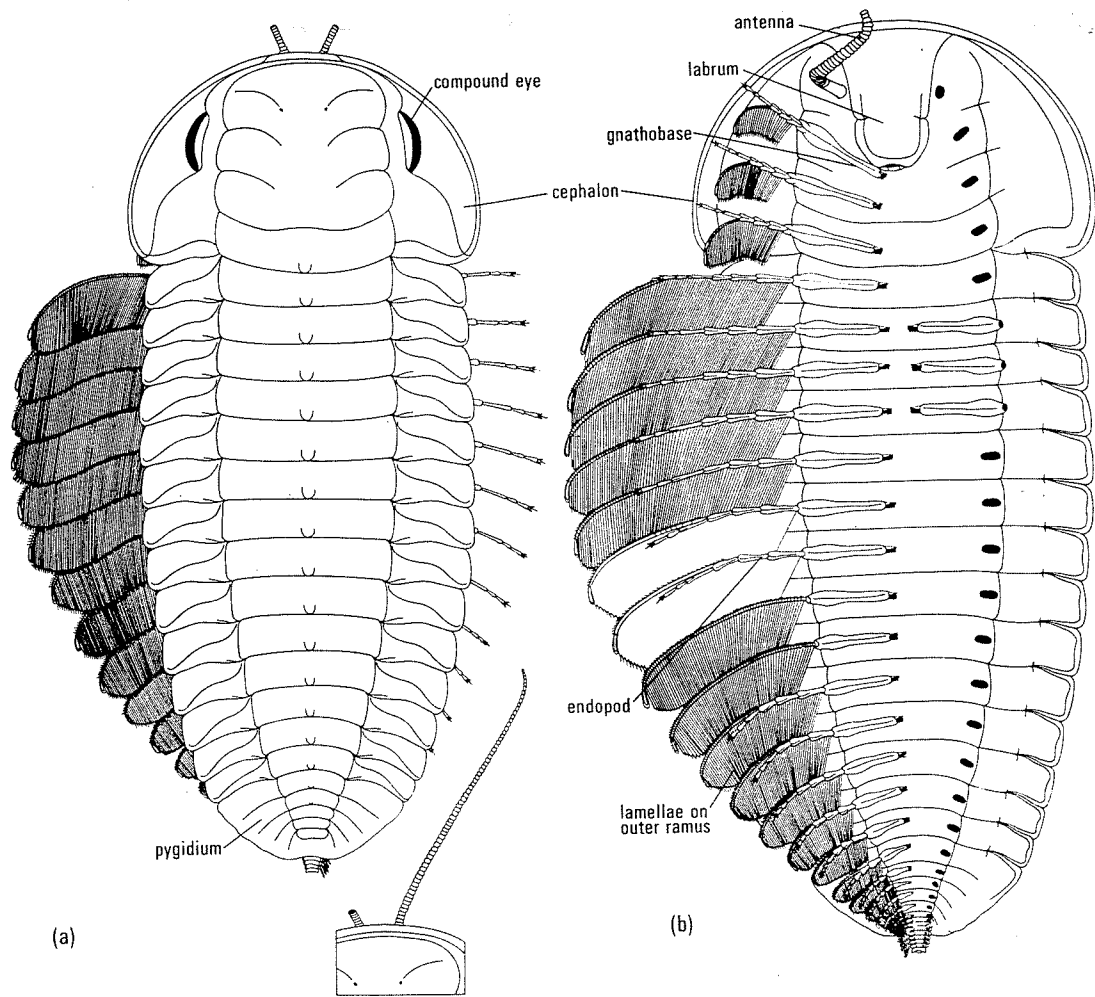
(a)

(b)

FIG. 1.3. The trilobite *Triarthrus eatoni* (Hall), 30 mm, Upper Ordovisian. (a) Dorsal, (b) ventral view. The endopods of the limb are shown entire on the left in (b) and projecting on the right in (a). The outer ramus of the limbs, bearing gill lamellae, are seen on the left in (a) and (b). The gnathobases from the coxae of all legs are shown on the left in (b) and the leg insertion, where legs are removed, are seen on the right in (b). Note the free trunk segments forming most of the body behind the head; the fused pygideal segments, five in number, at the hinder end. (After Cisne 1975.)
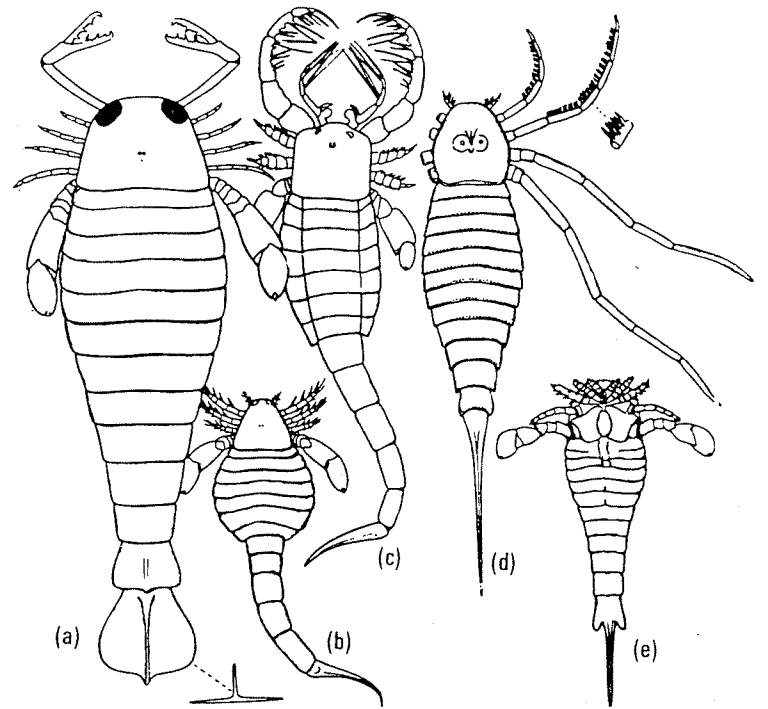

FIG. 1.11. Diversity of form in eurypterids. (a) *Jaekelopterus rhenaniae* (Jaekel), 1·8–1 m, Lower Devonian. (b) *Paracarcinosoma scorpionis* (Grote and Pitt), 1–0·4 m, Upper Silurian. (c) *Mixopterus kiaeri* Størmer, 1–0·67 m, Uppermost Silurian. (d) *Hallipterus excelsior* (Hall), 1·5–1 m, Devonian. (e) *Baltoeurypterus tetragonophthalmus* (Fischer), 1–0·24 m, Upper Silurian. (After Størmer 1944, in Tiegs and Manton 1958.)

Labels in figure (a): palp, oviger, chelophore

Labels in figure (b): oesophagus, intestine, muscle, muscle, ganglia of ventral chain, median proboscis nerve, proboscis ganglion
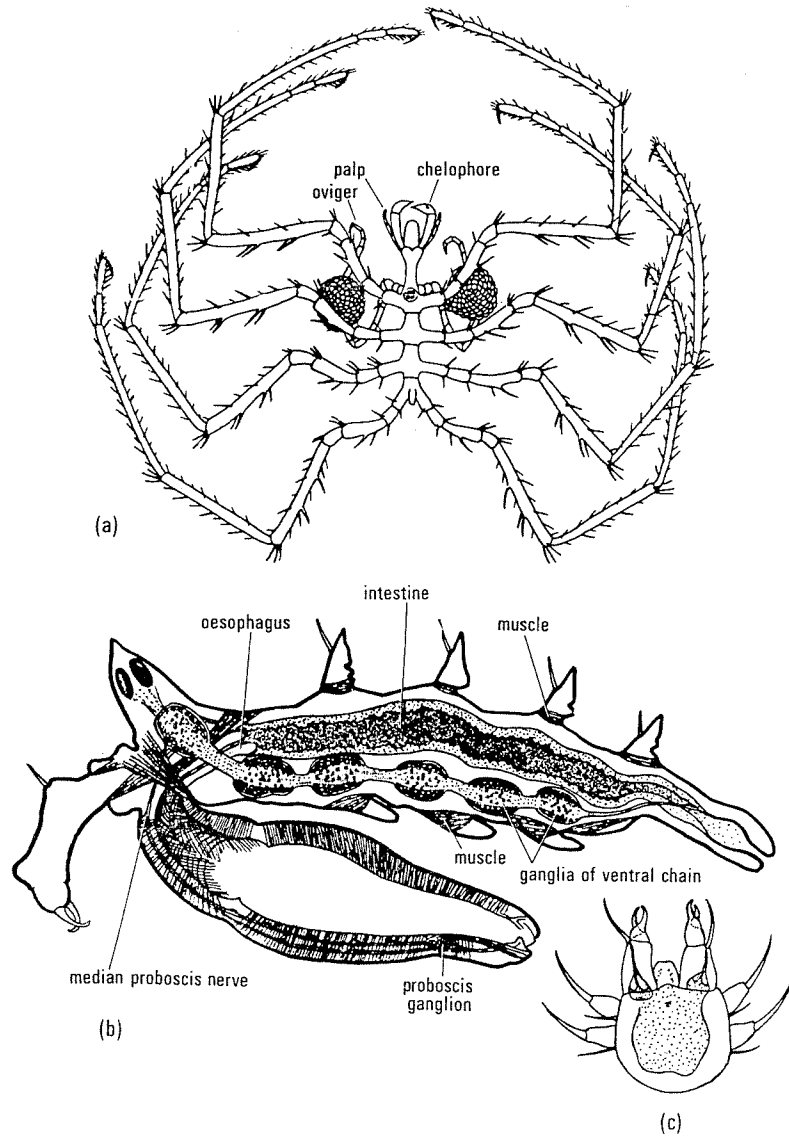
(a)

(b)

(c)

FIG. 1.16. Pycnogonida. (a) Dorsal view of *Nymphon rubrum* Hodge, 2 mm. (After Sars, from Tiegs and Manton 1958.) (b) Diagrammatic section of *Ascorhynchus castelli* (Dohrn). (After Dohrn, from Tiegs and Manton 1958.) (c) Protonymphon larva of *Pentanymphon antarcticum*. (After Hedgpeth 1947, from Tiegs and Manton 1958.)

Labels in figure (right): median ocelli, lateral eye, labrum, operculum, coxa, telson, outer branch leg 6, gill lamellae, outer ramus, endopod
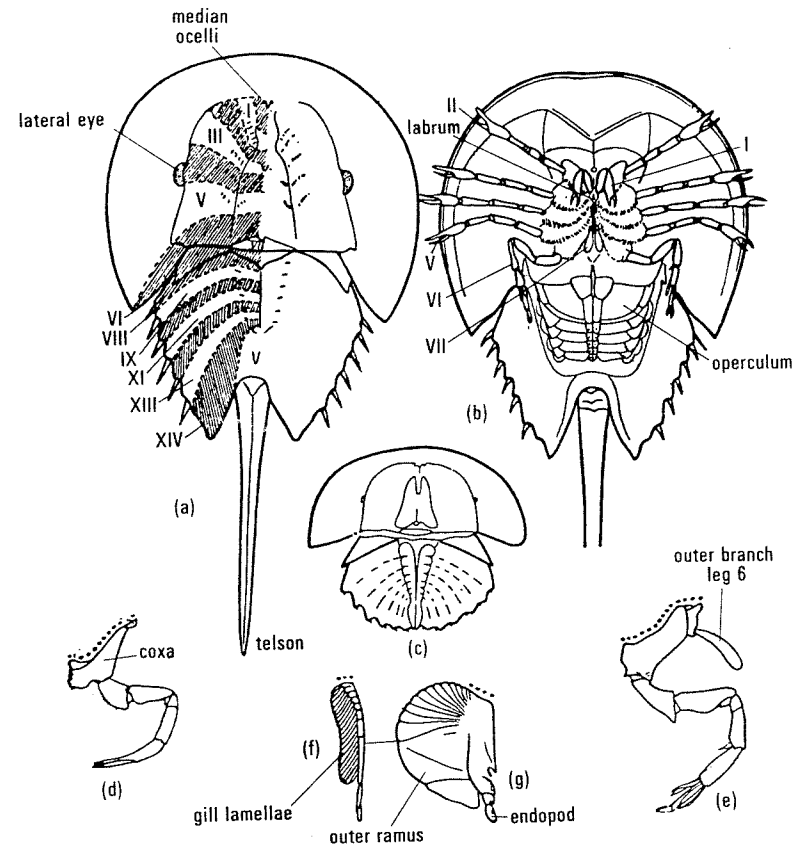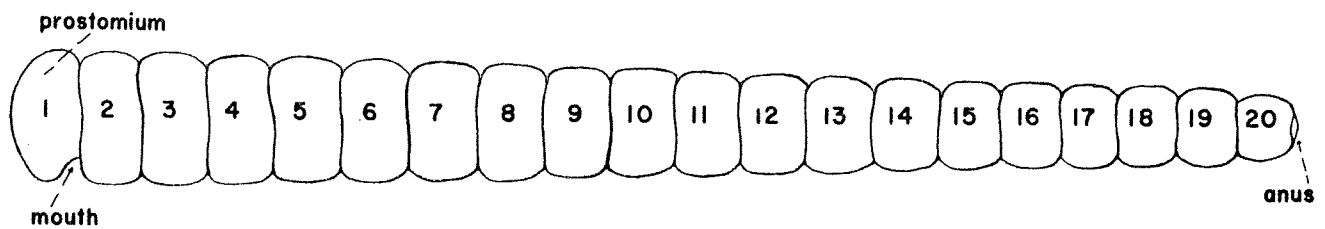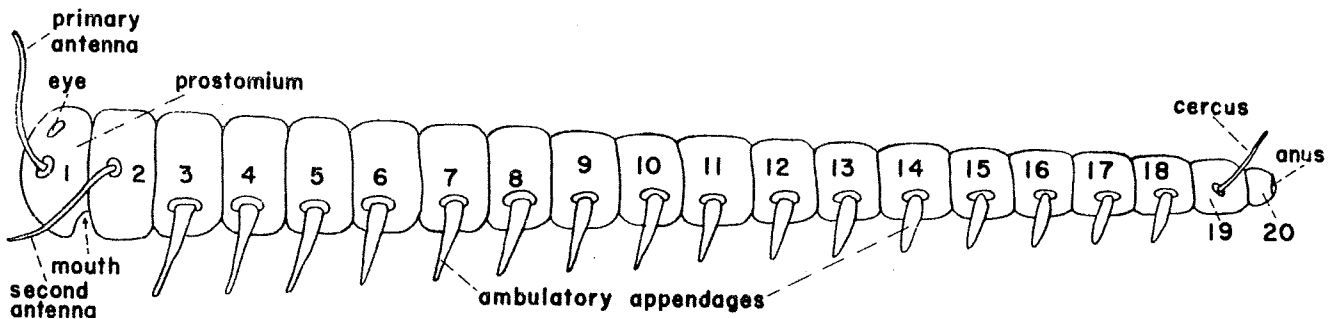
(a)

(b)

(c)

(d)

(e)

(f)

(g)

FIG. 1.9. *Limulus polyphemus* L. 450 mm. (a) Dorsal view. (b) Ventral view. (c) Larval stage. (d), (e) Fifth and sixth prosomal limbs respectively, coxa–body junction marked by dots. (f), (g) Mesosomal limb with respiratory gill lamellae, surface view in (g), longitudinal section through outer ramus in (f), coxa–body union marked by dots. (After Størmer 1944, from Tiegs and Manton 1958.)
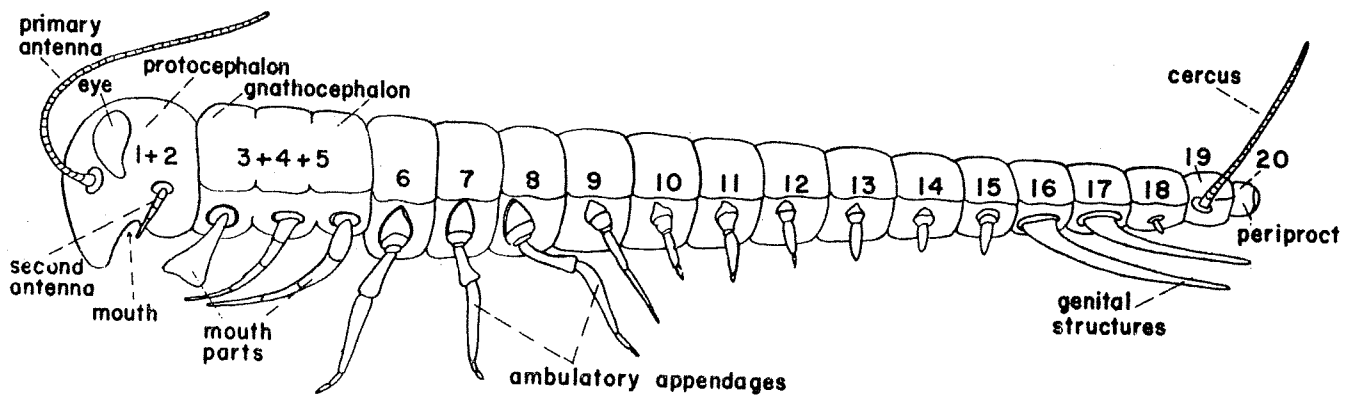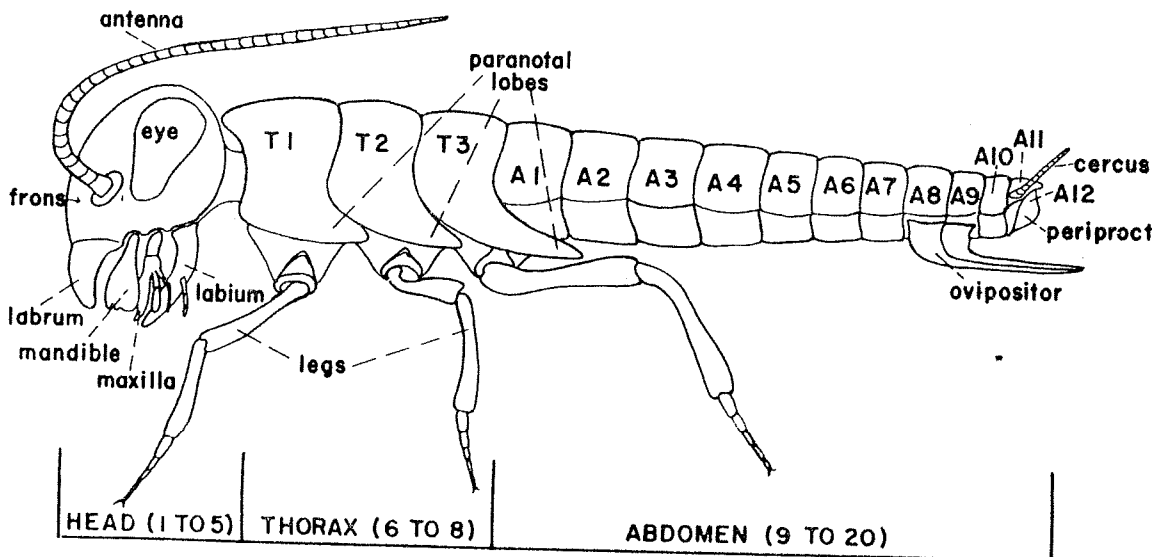
FIG. I - ORIGIN OF THE TAGMATA

prostomium

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |

mouth

anus

STAGE I - WORM-LIKE PROTOTYPE

primary antenna

eye   prostomium

cercus

mouth
second antenna

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |

anus

19 20

ambulatory appendages

STAGE II - DEVELOPMENT OF APPENDAGES

primary antenna

eye   protocephalon
       gnathocephalon

cercus

| 1+2 | 3+4+5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |

second antenna

mouth

mouth parts

ambulatory appendages

genital structures

periproct

STAGE III - CEPHALIZATION AND DIFFERENTIATION OF APPENDAGES

antenna

paranotal lobes

eye

frons

| T1 | T2 | T3 | A1 | A2 | A3 | A4 | A5 | A6 | A7 | A8 | A9 | A10 | A11 | A12 |

cercus

periproct

labrum
mandible
maxilla   labium

legs

ovipositor

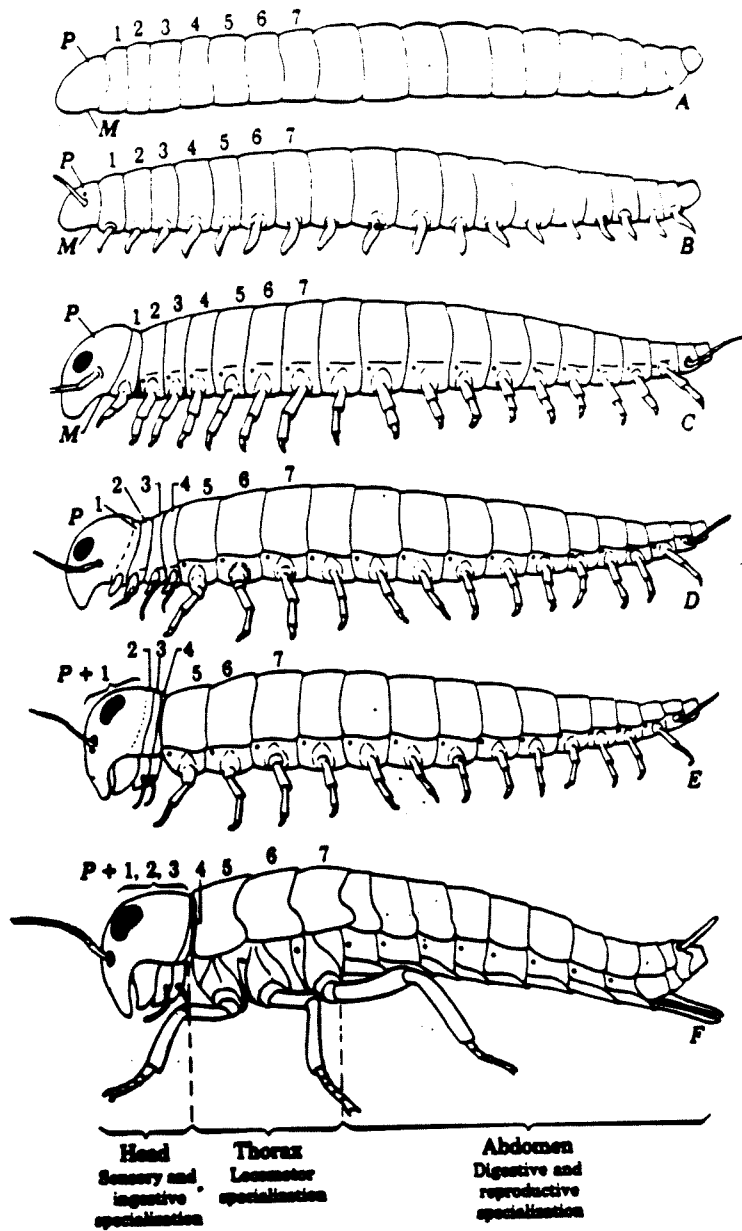| HEAD (1 TO 5) | THORAX (6 TO 8) | ABDOMEN (9 TO 20) |

STAGE IV - DIFFERENTIATION OF TAGMATA

Diagram showing hypothetical stages (*A* to *F*) in the development of body regions and appendages from a wormlike ancestor to an insect. *M*, mouth; *P*, prostomium. (Modified from Snodgrass)

ERAS	PERIODS		MOUNTAIN-MAKING EPISODES	LIFE	YEARS AGO
CENOZOIC	QUATERNARY	RECENT	ALPINE-CASCADIAN	AGE OF MAN	15,000
		PLEISTOCENE			1,500,000
	TERTIARY	PLIOCENE		AGE OF MAMMALS AND ANGIOSPERMS	
		MIOCENE			30,000,000
		OLIGOCENE			
		EOCENE	HIMALAYAN		
MESOZOIC	CRETACEOUS		LARAMIDE	AGE OF REPTILES AND GYMNOSPERMS	
	JURASSIC		SIERRA NEVADA		
	TRIASSIC				180,000,000
PALEOZOIC	"CARBONIFEROUS"	PERMIAN	APPALACHIAN HERCYNIAN		225,000,000
		PENNSYLVANIAN		AGE OF FISHES AND PTERIDOPHYTES	
		MISSISSIPPIAN			
	DEVONIAN				
	SILURIAN		CALEDONIAN-ACADIAN		370,000,000
	ORDOVICIAN				
	CAMBRIAN			AGE OF INVERTEBRATES AND THALLOPHYTES	
PROTEROZOIC	"PRE-CAMBRIAN"		GRAND CANYON YOUNGER LAURENTIANS		500,000,000
ARCHEOZOIC			OLDER LAURENTIANS		2,500,000,000?

Figure 1-2.   Subdivisions of geologic time. (Courtesy Darrah, W. C.: Principles of Paleobotany. 2nd Ed. Ronald Press, New York.)