INSECT – PLANT INTERACTIONS

INSECT – PLANT INTERACTIONS

2 broad categories of interactions

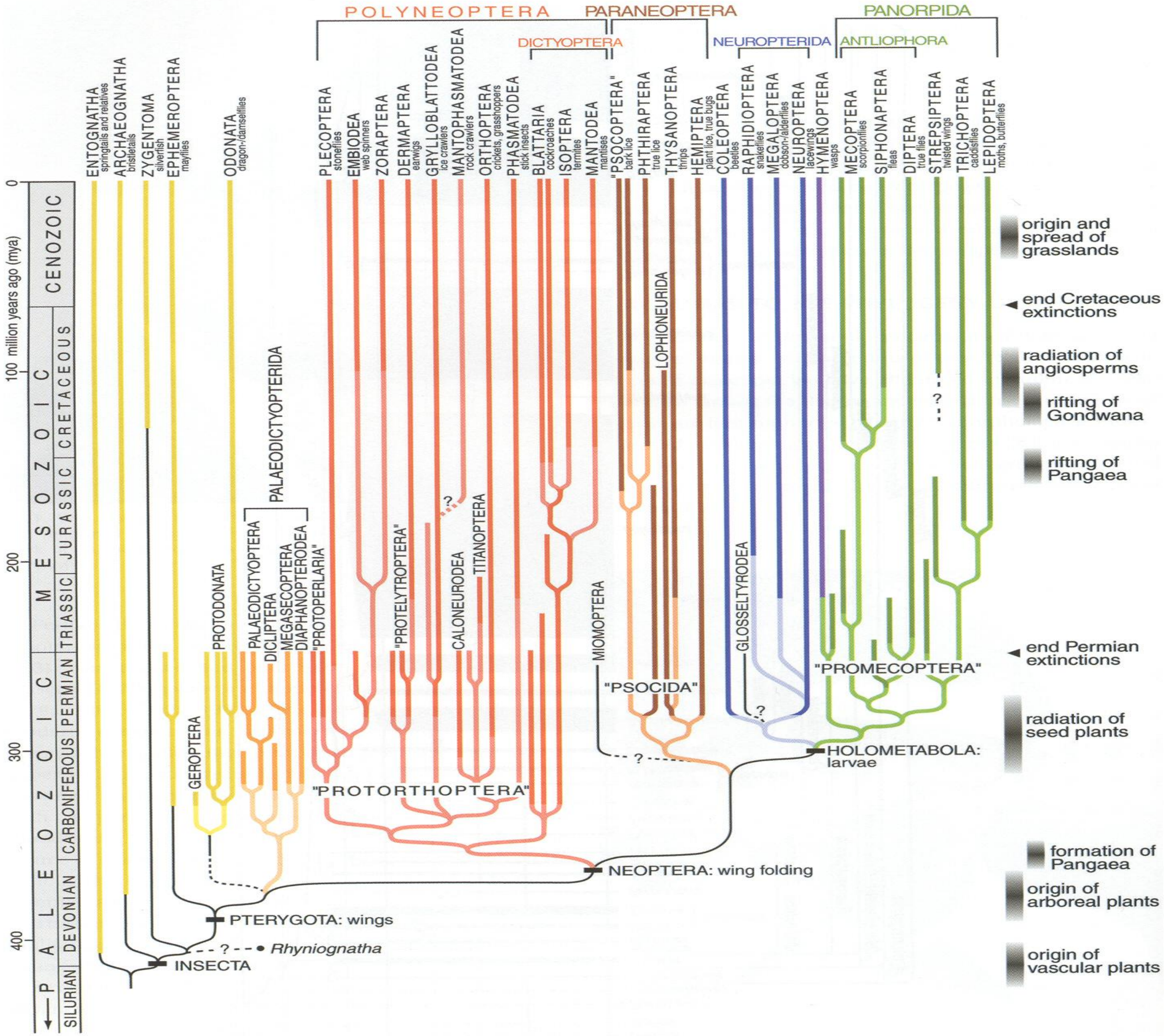
I. Herbivory (phytophagy)

leaf chewing, sap sucking, seed predation, gall inducing, leaf mining

II. Insect-plant mutualism

pollination and plant-insect food for defense relationships

What had that flower to do with being white
The wayside blue and innocent heal-all?
What brought the kindred spider to that height,
Then steered the white moth hither in the night?
What but design of darkness to appall?
If design govern a thing so small. – Robert Frost, *Design*



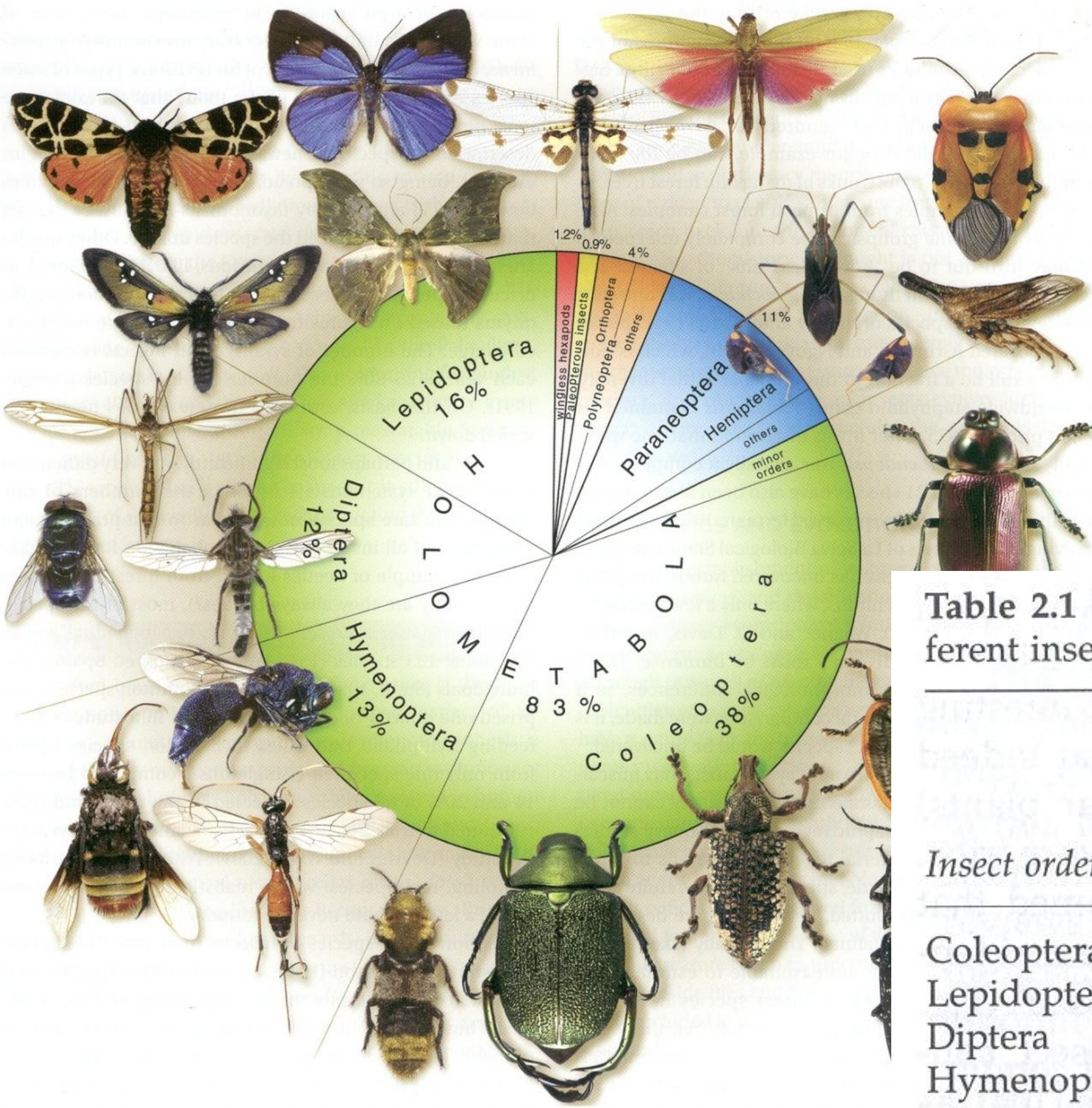
4.24. The phylogeny of living and extinct insect orders of insects used in this book, based on various sources (see text). Colors denote most major lineages; darker colors indicate the known extent of fossils.

RADIATIONS OF PHYTOPHAGOUS INSECTS

~ 10 – 25 % of tropical foliage is consumed by insects (not counting eating flowers, roots, stems, wood, seeds and fruit)

In temperate deciduous forests phytophagous insects comprise:
~25% of all arthropod species
~50% of arthropod biomass
~75% of arthropod individuals

In grasslands 10 – 75% of herbivory is by insects (vertebrates account for 15-35%)



1.6. The diversity of Recent hexapods as proportions of named species.

Table 2.1 Numbers of herbivorous species in different insect orders. (Data from various sources)

		Herbivorous species	
Insect order	*Total no. of species*	*No.*	*%*
Coleoptera	349 000	122 000	35
Lepidoptera	119 000	119 000	100
Diptera	119 000	35 700	30
Hymenoptera	95 000	10 500	11
Hemiptera	59 000	53 000	91
Orthoptera	20 000	19 900	100
Thysanoptera	5 000	4 500	90
Phasmida	2 000	2 000	100

RADIATIONS OF PHYTOPHAGOUS INSECTS

For extant species, phytophagous insects comprise ~43% of all insects

Primarily from:

Lepidoptera

Coleoptera

Hemiptera

Orthoptera

Hymenoptera

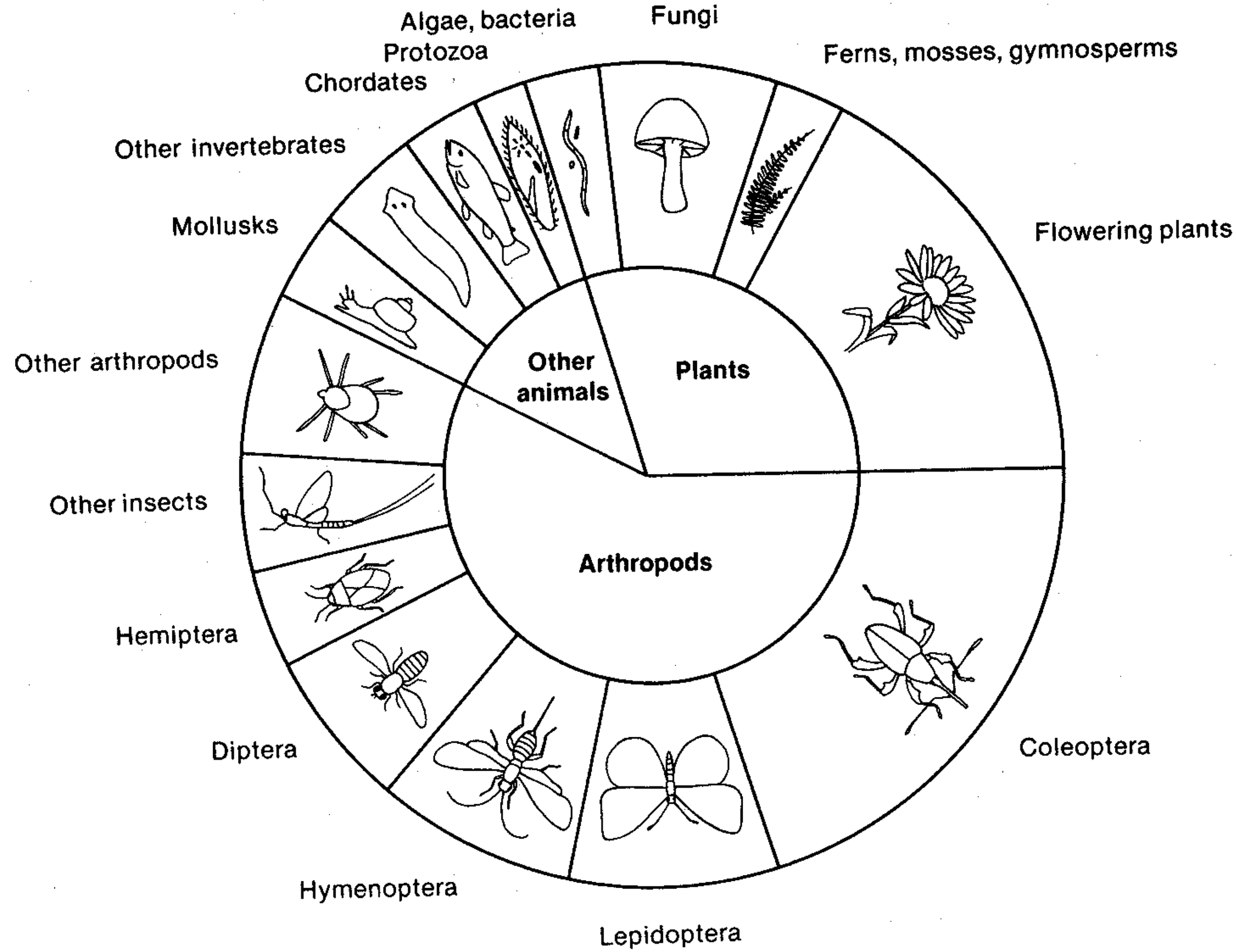


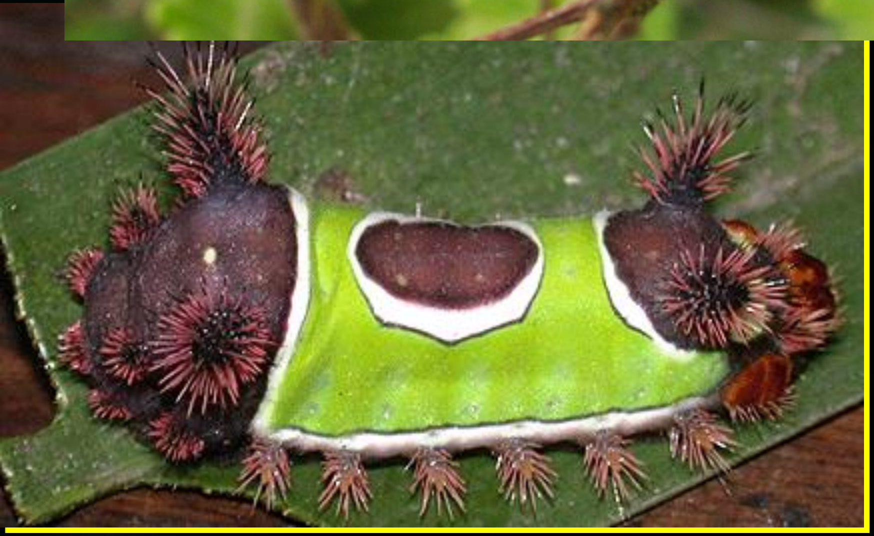
Figure 1.1 Relative numbers of species of arthropods, other animals, and plants.

RADIATIONS OF PHYTOPHAGOUS INSECTS

Lepidoptera – largest lineage of plant-feeding organisms;

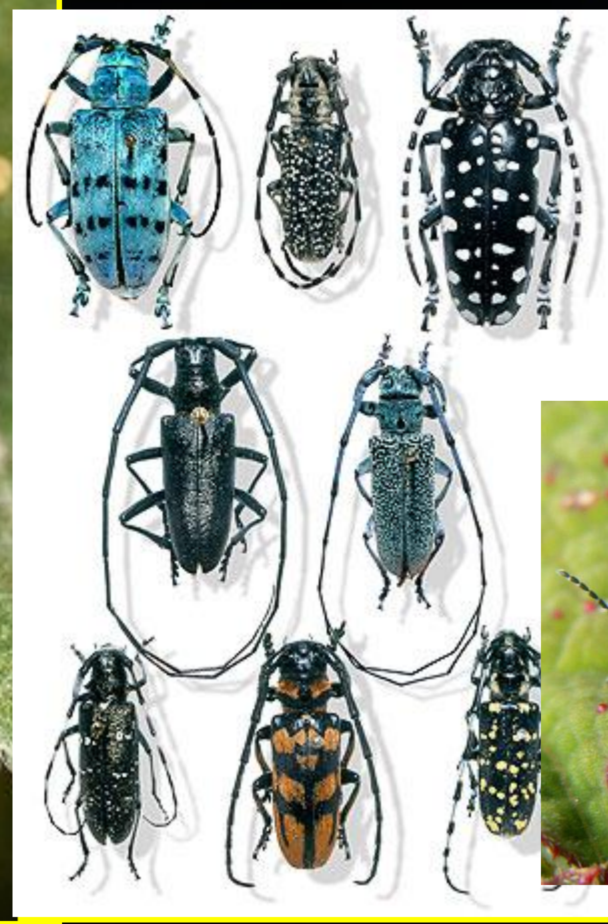
basal leps are detritivores (some phytophagous);

all others comprise a monophyletic group whose larvae are phytophagous (a few revisions to detritus and a few groups have become parasitoids and predators)



RADIATIONS OF PHYTOPHAGOUS INSECTS

Coleoptera – “Phytophaga” - Chrysomelidae, Curculionoidea, Cerambycidae …



RADIATIONS OF PHYTOPHAGOUS INSECTS

Hemiptera – Ancestrally all were phytophagous, virtually all Sternorrhyncha and Auchenorrhyncha are herbivores as are many families of the Heteroptera

Orthoptera – ~95% of orthopterans are herbivores. Closely related to the Phasmatodea all of which are herbivores

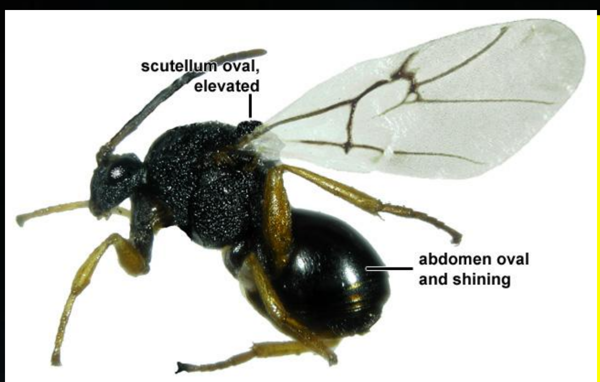
Fossil evidence suggests orthopteroid herbivory began in the Carboniferous – oldest living lineage of phytophagous insects

RADIATIONS OF PHYTOPHAGOUS INSECTS

Hymenoptera – Ancestrally all hymenopterans were phytophagous

Basal hymenopterans all eat plants

Secondary plant feeding by larval Cynipidae (galls), chalcid wasps (breeding w/in seeds), and assorted other groups like leaf-cutter bees and ants (although leaf-cutter ants use plants to grow fungus)

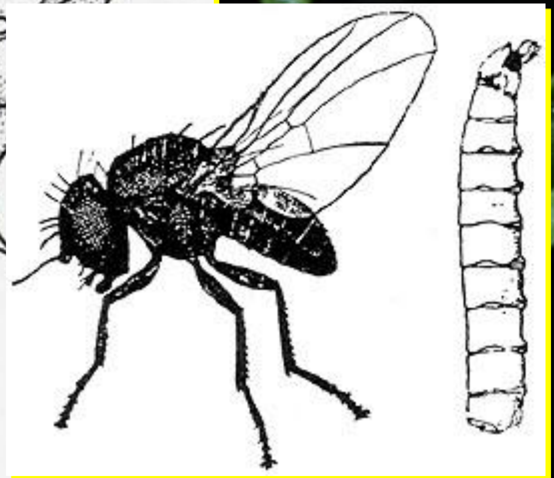


RADIATIONS OF PHYTOPHAGOUS INSECTS

Many other orders of insects contain herbivores
Among the smaller phytophagous lineages:

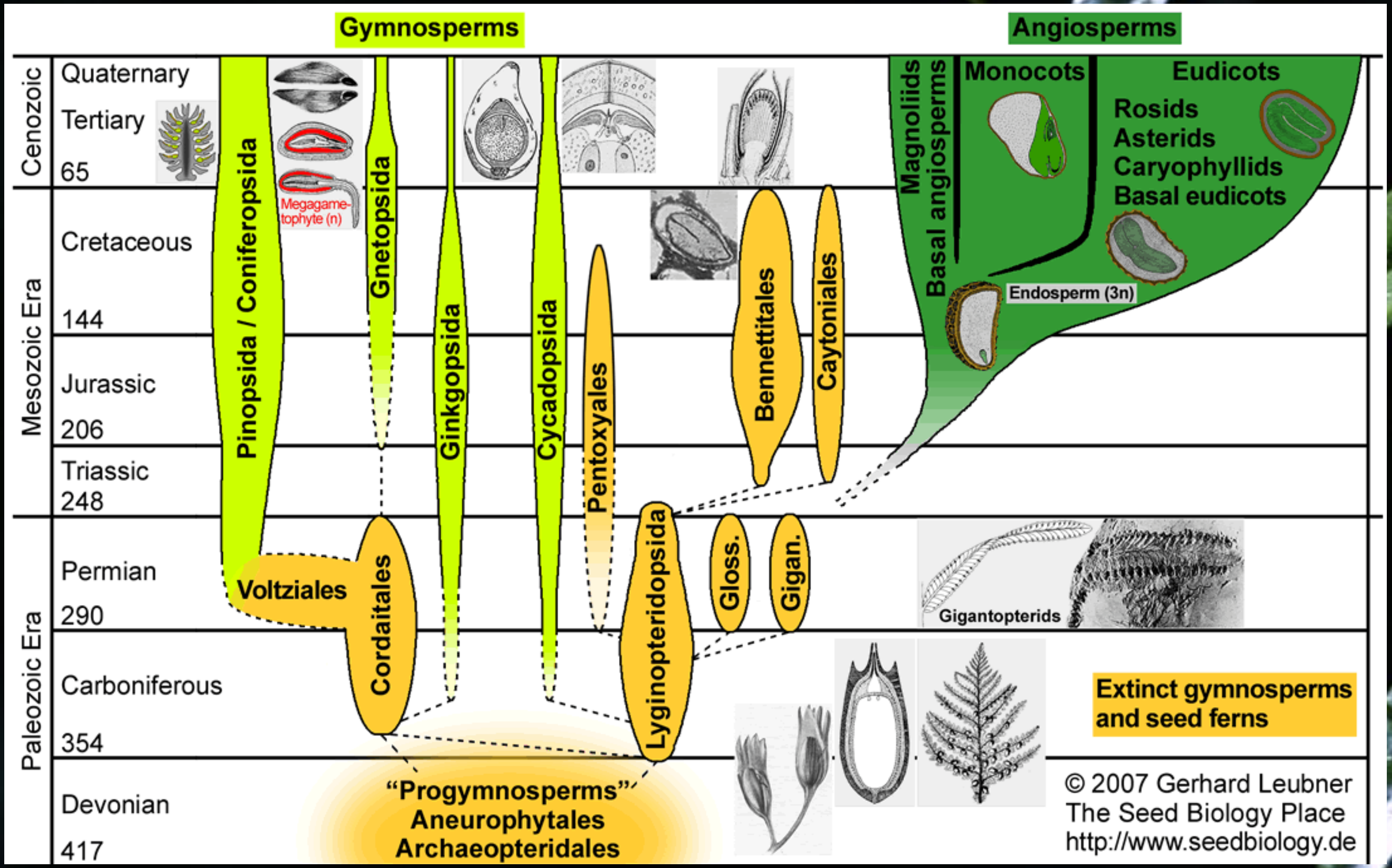
Thysanoptera – ancestral diet fungus but herbivory evolved several times

Phytophagy evolved several times in Diptera including, Cecidomyiidae (gall midges – largest herb lineage in flies), tephritoid fruit flies, agromyzid leaf miners, various Anthomyiidae and many families in Cyclorrhapha

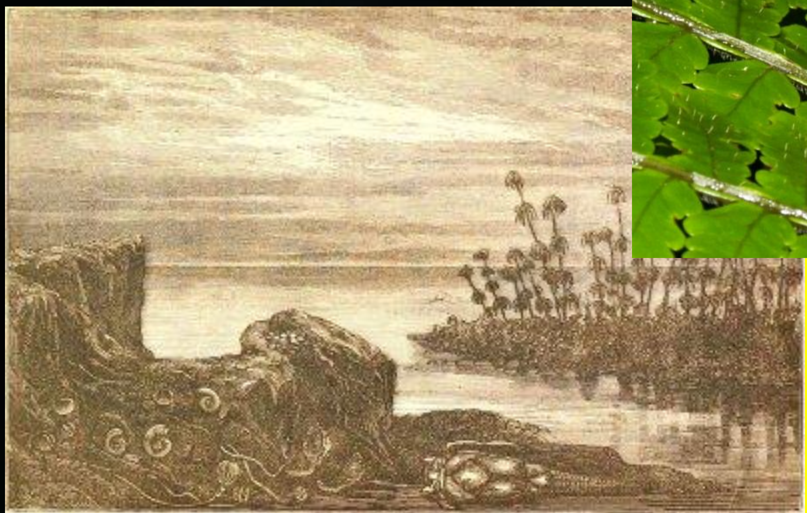


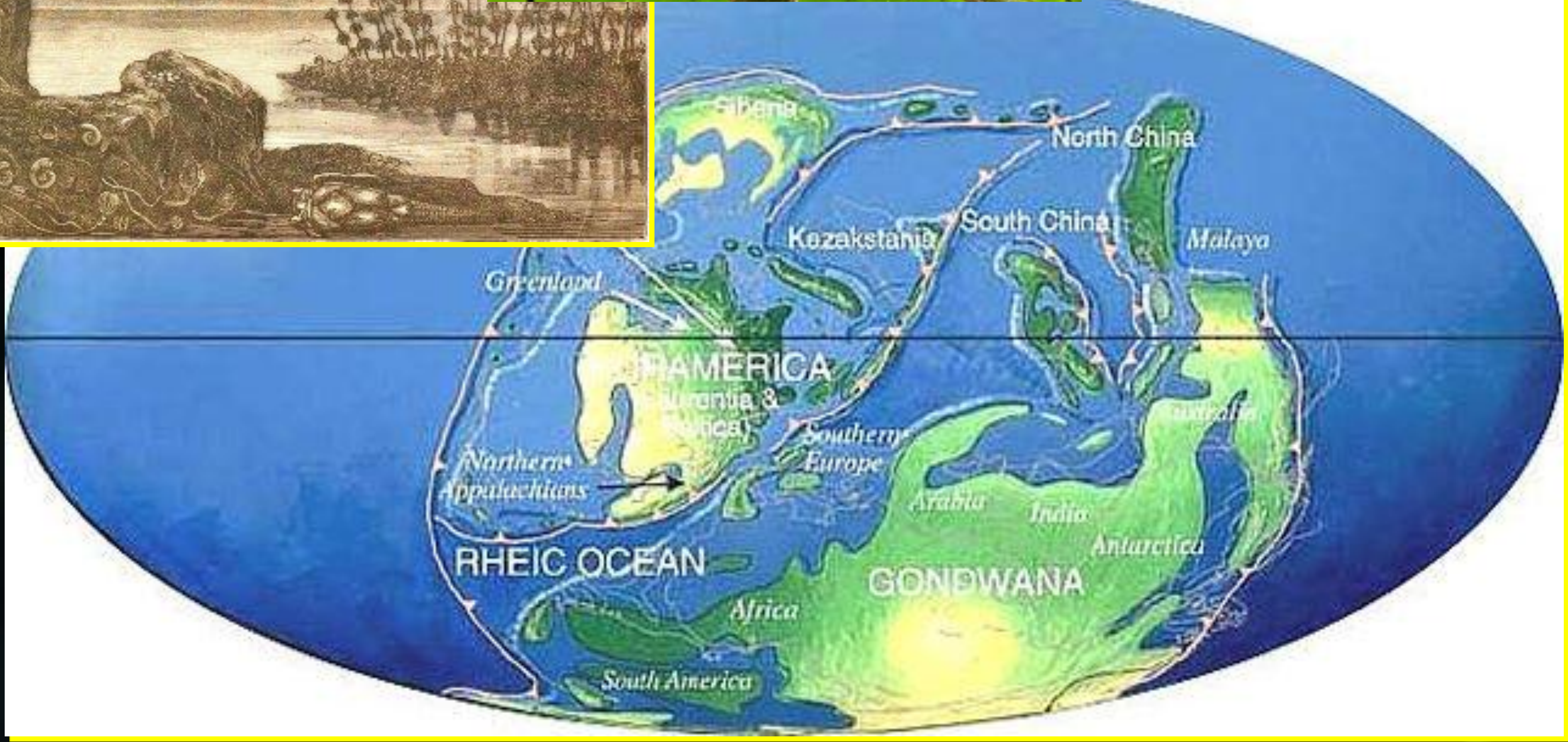
The host plants for these previous groups are primarily angiosperms.

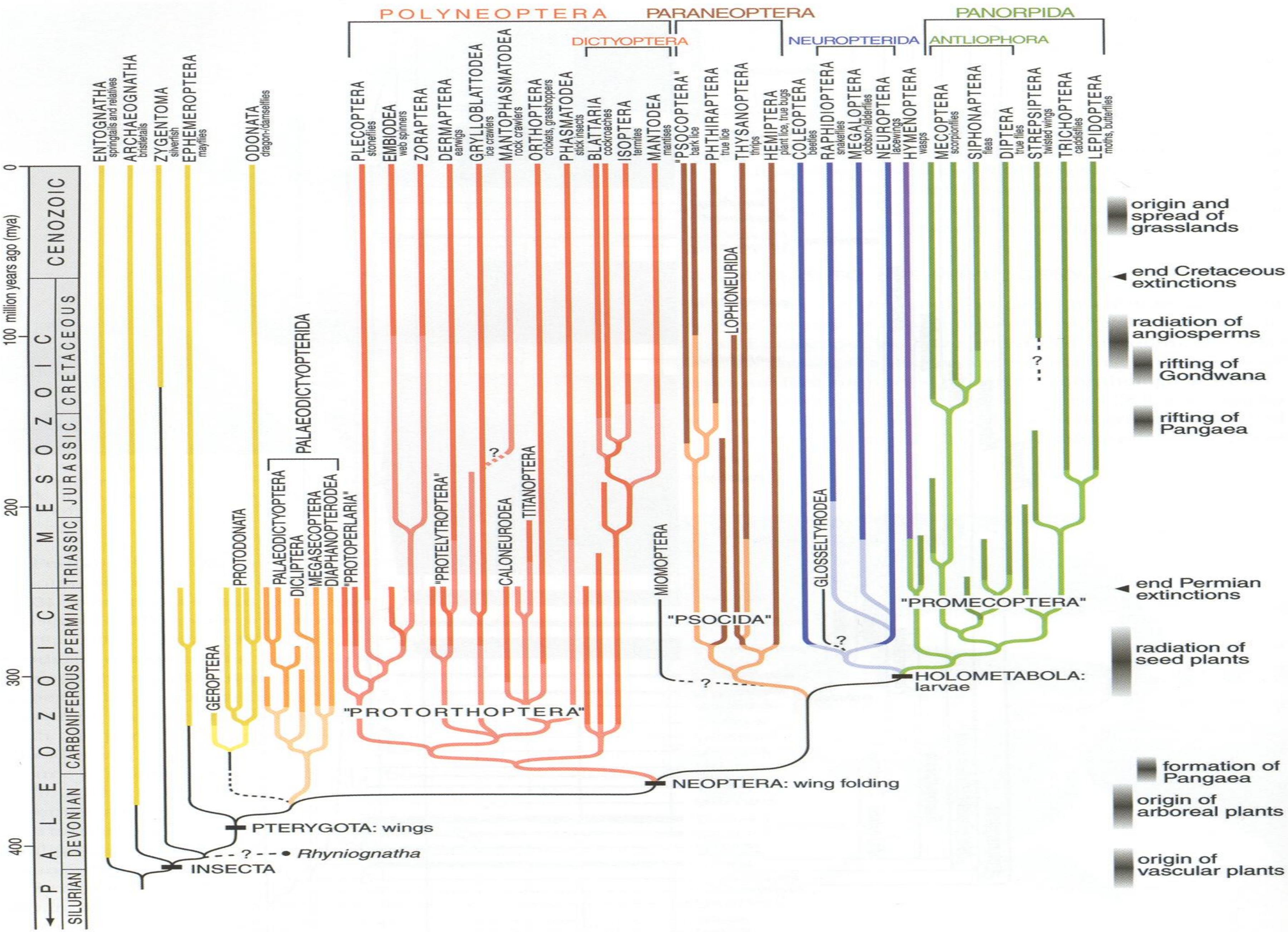
This may be due to the biomass and species dominance of angiosperms (i.e. the availability) or this may reflect the fact that angiosperms are more digestible and have higher nutritive value than gymnosperms.



Effects of plant-feeding insects are immense and have been taking place since the Devonian – 400 mya!! Most certainly since the Carboniferous (300 mya)







4.24. The phylogeny of living and extinct insect orders of insects used in this book, based on various sources (see text). Colors denote most major lineages; darker colors indicate the known extent of fossils.

- Modern non-insect hexapods and apterygotes scavenge in the soil and leaf litter on decaying plant material
- Earliest true insects probably fed similarly
- These habitats brought insects into close proximity to plant parts (i.e. roots, storage organs)
- Specialized use of plant shoots arose later in the phylogeny (~300 mya)

Feeding on plants presents problems not experienced by either scavengers living in soil, or by predators

1. **To eat shoots insects must gain and retain attachment plant (not a trivial issue)**

2. **Exposed on plant tissue may subject insect to greater desiccation**

3. **A diet of plant tissue (excluding seeds) is nutritionally inferior in proteins, sterol and vitamin content compared to food of animal or microbial origin**

4. **Plants are not passive recipients of herbivory**
   - **Physical defense (spines, spicules)**
   - **Chemical defense (repel, poison, reduce digestibility or somehow interfere with insect behavior and/or physiology**

Plant defenses against herbivory

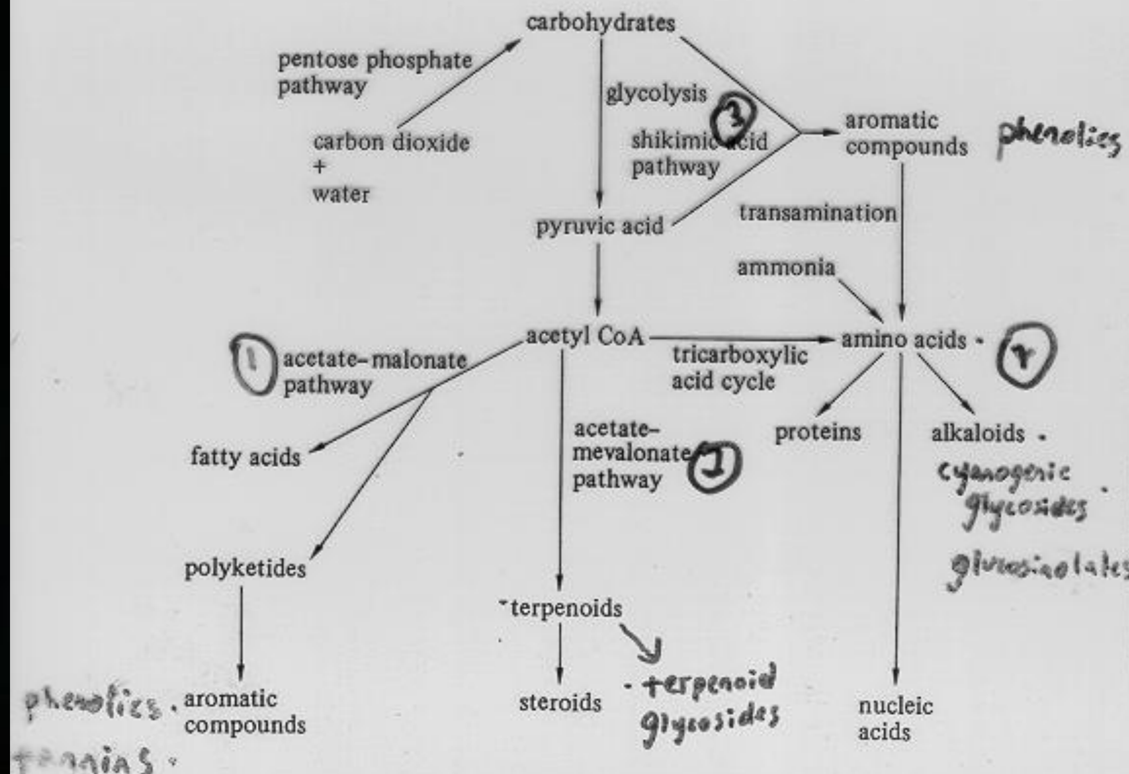


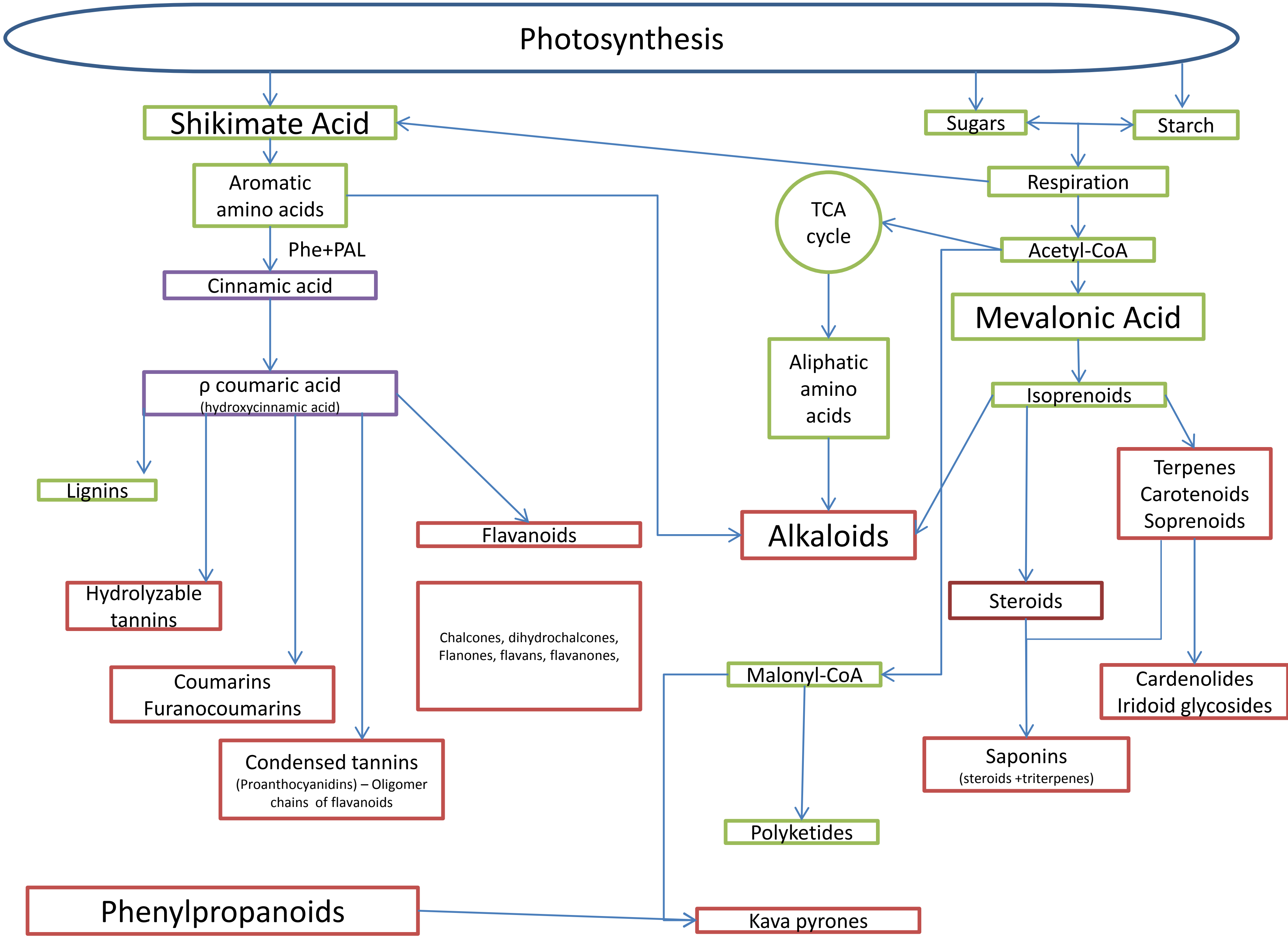
Figure 1.1 Biosynthetic pathways in plants.

Chapters 3, 5 and 6, respectively), which are interrelated as shown in *Figure 1.1*. These pathways are ubiquitous and the first products formed in quantity can be considered primary metabolites. Thus, palmitic acid (1.2) is the primary metabolite of the acetate-malonate pathway, other fatty acids and their derivatives being secondary metabolites.

$$CH_3(CH_2)_{14}COOH$$

palmitic acid
(1.2)

The terpenoids can be chemically and biochemically divided into classes depending on the number of C_5 isoprene units they contain, each class being derived from a primary metabolite precursor biosynthesised by the acetate–mevalonate pathway. Thus, geranyl pyrophosphate (1.3) is the primary metabolite from which the monoterpenoids are derived, farnesyl pyrophosphate (1.4)

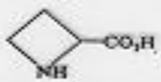


Photosynthesis
Shikimate Acid
Sugars
Starch
Respiration
Aromatic amino acids
TCA cycle
Acetyl-CoA
Phe+PAL
Cinnamic acid
Mevalonic Acid
Aliphatic amino acids
ρ coumaric acid
(hydroxycinnamic acid)
Isoprenoids
Terpenes
Carotenoids
Soprenoids
Lignins
Flavanoids
Alkaloids
Hydrolyzable tannins
Chalcones, dihydrochalcones,
Flanones, flavans, flavanones,
Steroids
Coumarins
Furanocoumarins
Malonyl-CoA
Cardenolides
Iridoid glycosides
Condensed tannins
(Proanthocyanidins) – Oligomer chains of flavanoids
Saponins
(steroids +triterpenes)
Polyketides
Phenylpropanoids
Kava pyrones

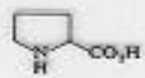
Table 3.1 Some nitrogen-based toxins in plants

Class of compound	Example(s)	Toxicity
Non-protein amino acids	L-DOPA in *Mucuna* seed	Insects, espec. bruchid beetles
	β-Cyanoalanine in *Vicia* seed	Fatal dose in rats 200 mg/kg body wt
Cyanogenic glycosides	Linamarin and lotaustralin in *Lotus corniculatus*	Universal; fatal dose of HCN in man *ca* 50 mg
Glucosinolates	Sinigrin in *Brassica*	Cattle and insects
Alkaloids	Senecionine in ragwort *Senecio jacobaea* leaves	Espec. cattle
	Atropine in *Atropa belladonna* berries	Mammals, but not birds; LD_{50} in rats 750 mg/kg
Peptides	Amanitine in *Amanita phalloides*	Mammals
	Viscotoxin in *Viscum album* berries	Animals, but not birds
Proteins	Abrin in *Abrus precatorius*	Lethal dose in man 0·5 mg
	Phytohaemagglutinin in *Phaseolus vulgaris*	Bruchid beetles

Non-protein amino acid	Protein amino acid
$NCCH_2CHNH_2CO_2H$	$CH_3CHNH_2CO_2H$
β-cyanoalanine	alanine



azetidine 2-carboxylic acid



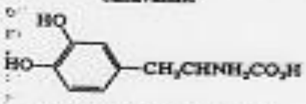
proline

$NH_2C{=}NH.NHO(CH_2)_2CHNH_2CO_2H$

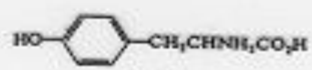
canavanine

$NH_2C{=}NH.NH(CH_2)_3CHNH_2CO_2H$

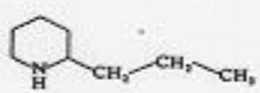
arginine



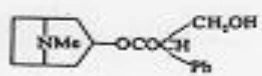
3,4-dihydroxyphenylalanine (L-DOPA)



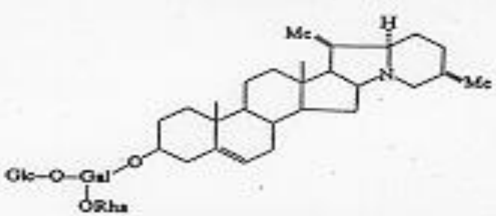
tyrosine



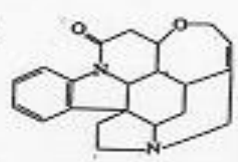
coniine, of *Conium maculatum* (Umbelliferae)



atropine, of *Atropa belladonna* (Solanaceae)



solanine, of *Solanum tuberosum* (Solanaceae)

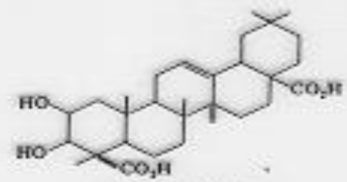


strychnine, of *Strychnos nux-vomica* (Loganaceae)

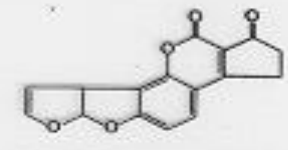
Fig. 3.2 Some characteristic alkaloids of plants

Table 3.2 Some non-nitrogenous toxins in plants

Class of compound	Example	Toxicity
Iridoids	Aucubin in *Aucuba japonica* leaves	Insects, birds
Sesquiterpene lactones	Hymenovin in *Hymenoxys odorata*	Livestock and insects
Cardiac glycosides	Ouabain in *Acokanthera ouabaio*	Heart poison, LD_{50} in rats 17·2 mg/kg
Saponins	Medicagenic acid in *Medicago sativa* leaves	Fish, insects
Furanocoumarins	Xanthotoxin from *Pastinaca sativa*	Insects
Isoflavonoids	Rotenone in derris root	Mainly insects and fish
Quinones	Hypericin in *Hypericum perforatum* leaves	Mammals, especially sheep
Polyacetylenes	Oenanthetoxin in *Oenanthe crocata* roots	Mammals
Aflatoxins	Aflatoxin B_1 from *Aspergillus flavus* infection on peanut	Birds and mammals



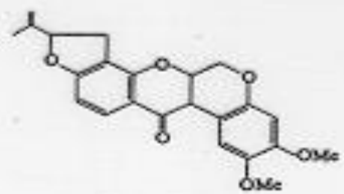
medicagenic acid, from *Medicago sativa* (lucerne)



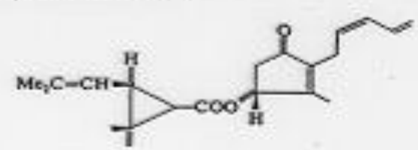
aflatoxin B_1, from *Aspergillus flavus* growing on peanuts *Arachis hypogea*

$HOCH_2CH{=}CH(C{\equiv}C)_2(CH{=}CH)_2(CH_2)_3CHOH(CH_2)_2CH_3$

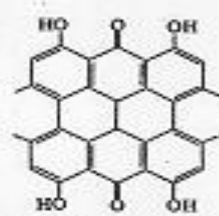
oenanthotoxin, from *Oenanthe crocata*



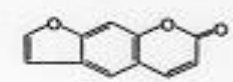
rotenone, from *Derris* root



pyrethrin I, from *Chrysanthemum cinerariifolium*

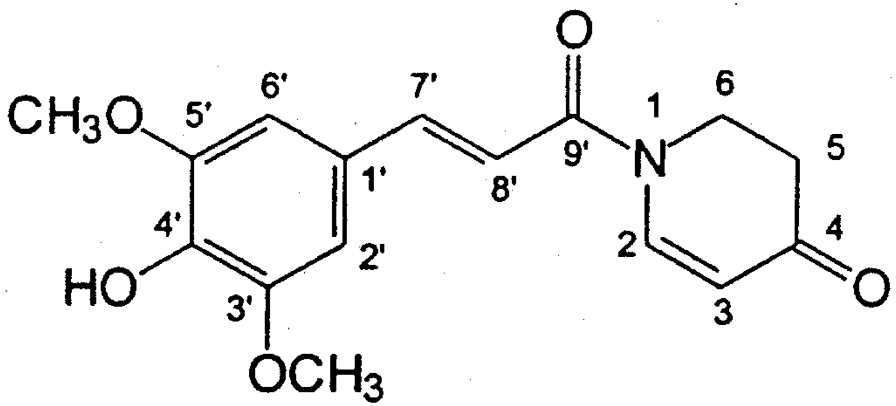


hypericin, from *Hypericum perforatum* (St. Johns wort)

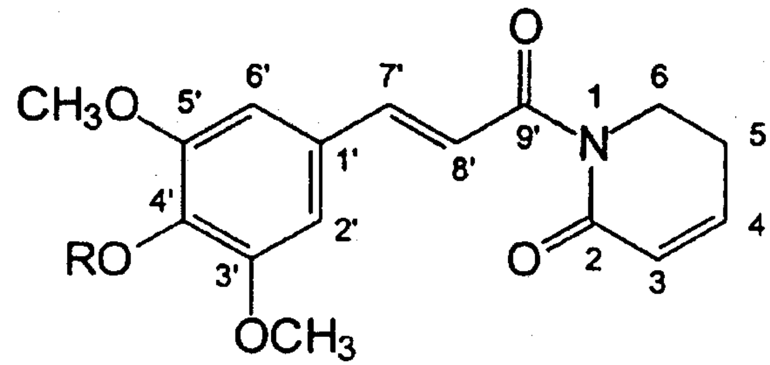


psoralen from umbellifer leaves and stems

Fig. 3.4 Some non-nitrogenous plant toxins



3



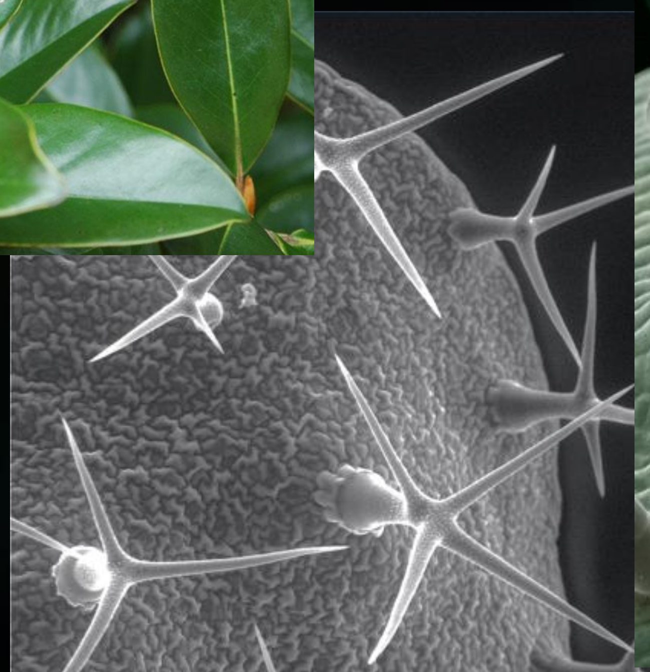
1 R = CH_3

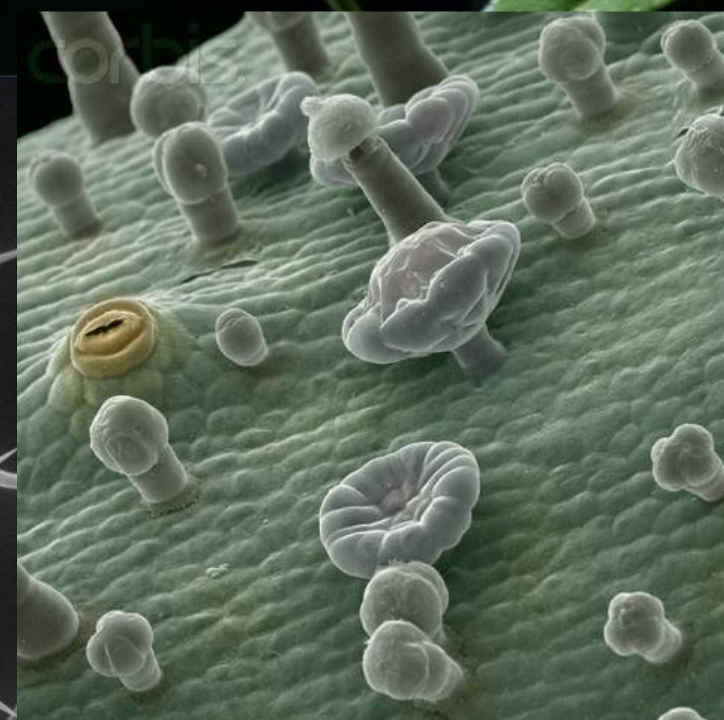
2 R = H

RADIATIONS OF PHYTOPHAGOUS INSECTS

Given these hurdles to herbivory, plants represent an adaptive free zone

Those that have jumped the hurdle have radiated…





Herbivory

- Plants are suboptimal food
  - Dilute nutrients in indigestible structural compounds (e.g. cellulose, lignin).
  - Secondary metabolites cause toxicity (qualitative) or indigestibility (quantitative).
  - Spines or pubescence on stems and leaves

Selection Pressure Exerted By Herbivorous Insects on Plants

- Resistance vs. Defense
- Plant apparency hypothesis
  - ‘Apparent plants’ → quantitative defense (tannins)
  - ‘Non-apparent plants’ → qualitative defenses (alkaloids)
- Resource availability hypothesis
  - Availability of resources determines amount and type of defense

Palaeogeography, Palaeoclimatology, Palaeoecology 321–322 (2012) 102–112

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Plant–arthropod associations from the Early Miocene of the Most Basin in North Bohemia—Palaeoecological and palaeoclimatological implications

Stanislav Knor [a,*], Jakub Prokop [a], Zlatko Kvaček [b], Zdeněk Janovský [c], Torsten Wappler [d]

[a] Charles University, Faculty of Science, Department of Zoology, Viničná 7, CZ-128 44, Praha 2, Czech Republic
[b] Charles University, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, CZ-128 43 Praha 2, Czech Republic
[c] Charles University, Faculty of Science, Department of Botany, Benátská 2, CZ-128 01, Praha 2, Czech Republic
[d] Steinmann Institute for Geology, Mineralogy and Palaeontology, Division Palaeontology, University of Bonn, Nussallee 8, D-53115 Bonn, Germany

ARTICLE INFO

Article history:
Received 8 August 2011
Received in revised form 16 January 2012
Accepted 22 January 2012
Available online 31 January 2012

Keywords:
Most Basin
Early Miocene
Herbivory
Plant–insect interactions
Climate change
Palaeobotany
Palaeoecology

ABSTRACT

Terrestrial plants and insects account for the majority of the Earth's biodiversity today, and herbivorous interactions are dated back more than 400 million yr. However, investigation of their associations remains in its infancy in Europe. The Miocene is characterized by palaeogeographic re-organization due to the collision of the African with the Eurasian plates. Antarctica's enormous impact on global climatic conditions, and thus on European palaeoenvironment, resulted from a series of episodes of minor glaciations in the Early Miocene after the initial cooling and ice sheet formed during the Oligocene.

More than 3500 plant remains showing various kinds of feeding damage were available for the present study. These trace fossils are classified according to their external morphology into damage types (DT) and grouped to functional feeding-groups. The Neogene plant record in Europe is rich and diverse, offering a profound large-scale understanding of the floristic and vegetational development. A database of fossil traces from the Most Basin was compiled and analyzed by various statistical methods in terms of the diversity and intensity of palaeoherbivory. The primary objective is to present results on the development of insect herbivory through the section of the Bílina Mine in North Bohemia, with the aim of understanding the principal factors that caused the observed phenomena. The research was focused on two horizons—Delta Sandy Horizon (DSH) and Lake Clayey Horizon (LCH)—both sufficiently represented to compare their palaeoecological and palaeoclimatological signals on the basis of the presence of damages caused by insects and other herbivorous arthropods. A total sample of 60 different damage types, attributed to eight main functional feeding groups, was examined. Results from analyses of the frequency and diversity of the selected categories of plant arthropod associations within both examined horizons significantly support different environmental conditions. The LCH seems to be affected by the relatively colder and drier climatic conditions as indicated by a four times greater frequency of leaves with galls and lower taxonomic diversity and species equability, whereas DSH indicates warmer and more humid conditions reflecting the higher diversity of the plant species and damage types.

1. Introduction

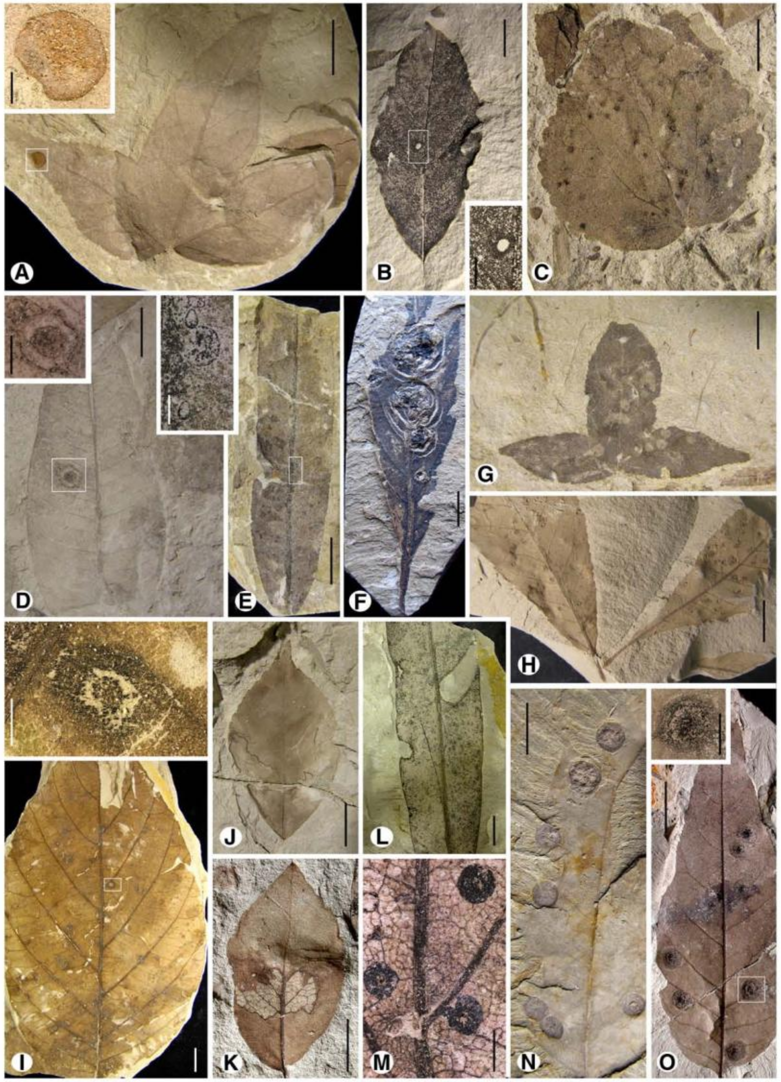
The ecology of plant–insect associations currently is a significant aspect of modern ecological research. Consequently, studies of insect herbivory on fossil leaves provide crucial information on the ecology of feeding associations and the association of plants and their insect herbivores that cannot otherwise be obtained separately from the record of plant macrofossils and insect body fossils. Because food webs incorporating plants and phytophagous insects account for up to 75% of global diversity, it is essential to examine how factors like global warming and cooling affect insect herbivory.

The Earth's climate was gradually cooling during the Tertiary (the last 65 Ma). This trend was punctuated by three more abrupt cooling steps (e.g., Zachos et al., 2001a). Palaeoclimate indicators suggest that the East Antarctica ice-sheet formation, which initiated in the Late Oligocene (Lyle et al., 2007), resulted in a decrease in global sea level by nearly 70 m during this time (Berggren et al., 1995; Berggren, 2002). Subsequently, in the Miocene important vegetation changes resulted from this altered global climate (Utescher et al., 2011, and references herein). These changes were mainly triggered by fluctuations in and later expansion of the Antarctic continental ice-sheet (Barker and Thomas, 2004; Shevenell et al., 2004). Except at the very beginning of the Early Miocene, the glaciation of Antarctica was ephemeral and unstable compared to the present extent (Naish et al., 2001) and the Northern Hemisphere was largely ice-free at that time (Billups, 2002, and references therein). The Early to Middle Miocene

* Corresponding author. Tel.:+420 221951837; fax: +420 221951840.
E-mail address: knor@natur.cuni.cz (S. Knor).

0031-0182/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2012.01.023

0.9% of damaged leaves exhibit four types. The five most abundant host plant taxa, accounting for one-quarter of the fossil leaves in the DSH, are affected by more than 30.6% of insect damage occurrences documented therein (Fig. 3A). *Alnus julianiformis* is the most abundant taxon (7.4%) in the DSH and is also one of the most consumed species (31.9%). The corresponding diversity of 19 different types of damage is the highest in the whole assemblage. Second in order of most numerous taxa, *Ulmus pyramidalis* (5.3%) represents a considerably lower proportion of damaged leaves (14.4%) and absolute diversity of types of damage. Three other similarly numerous taxa—*Acer tricuspidatum* (4.1%), *Nyssa Haidingeri* (3.9%), and *Alnus gaudini* (3.8%) exhibit a similar proportion of damaged leaves (27.5%, 20.7%, and 28.2%). *Populus zaddachii* var. *brabenecii* has the highest level of damage (56.8%) among the taxa that count 25 and more specimens



Dyer, L.A., Letourneau, D.K., Vega Chavarria, G. and D. Salazar Amoretti. 2010. Herbivores on a dominant understory shrub increase local plant diversity in rain forest communities. ***Ecology*** 91:3707-3718.

Physimera **sp. (Chrysomelidae) on** *P. imperiale*

Types of Herbivory – Chewers

Chewers - Most diverse of the leaf-chewing insects are the Coleoptera and Lepidoptera.

Other important groups--Orthoptera, Hymenoptera, Phasmatodea

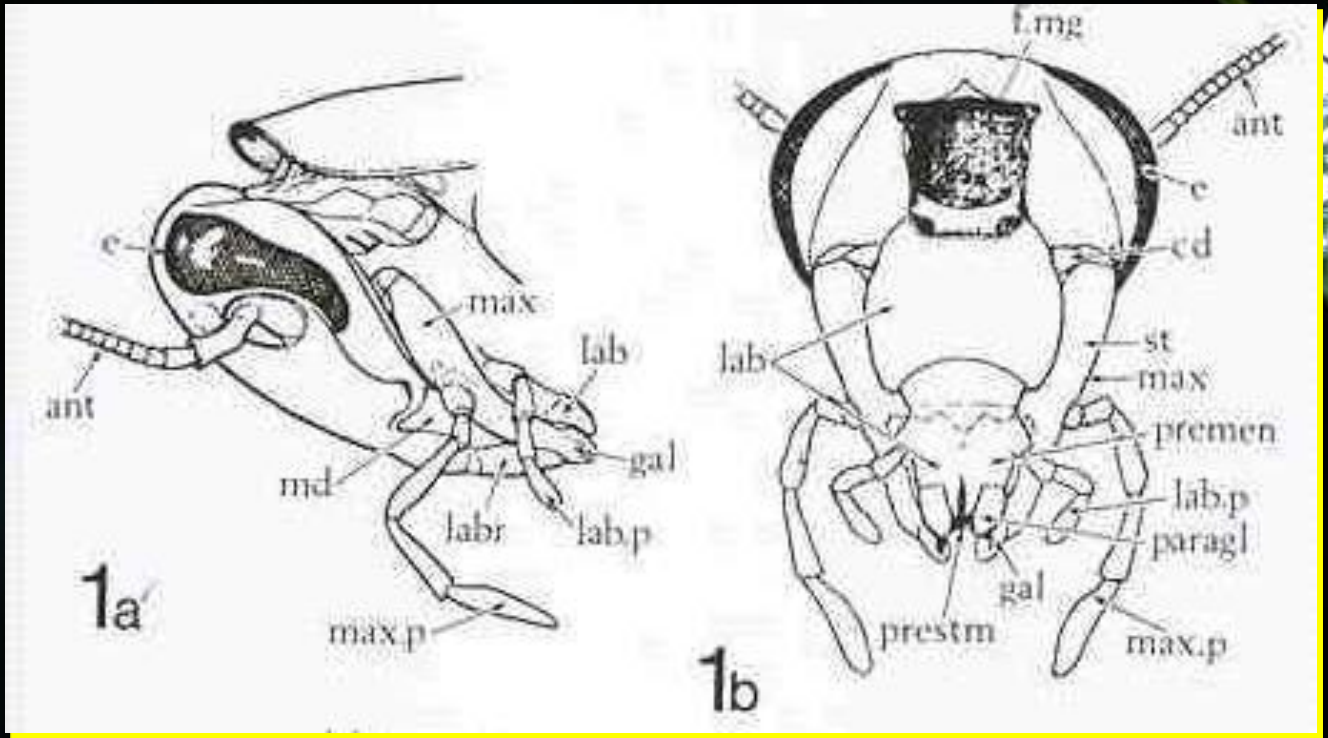
Insects eat leaves, roots, shoots, stems, and flowers or fruits

Chewing insects possess mandibulate mouthparts.

Mandibles serve to cut and grind food

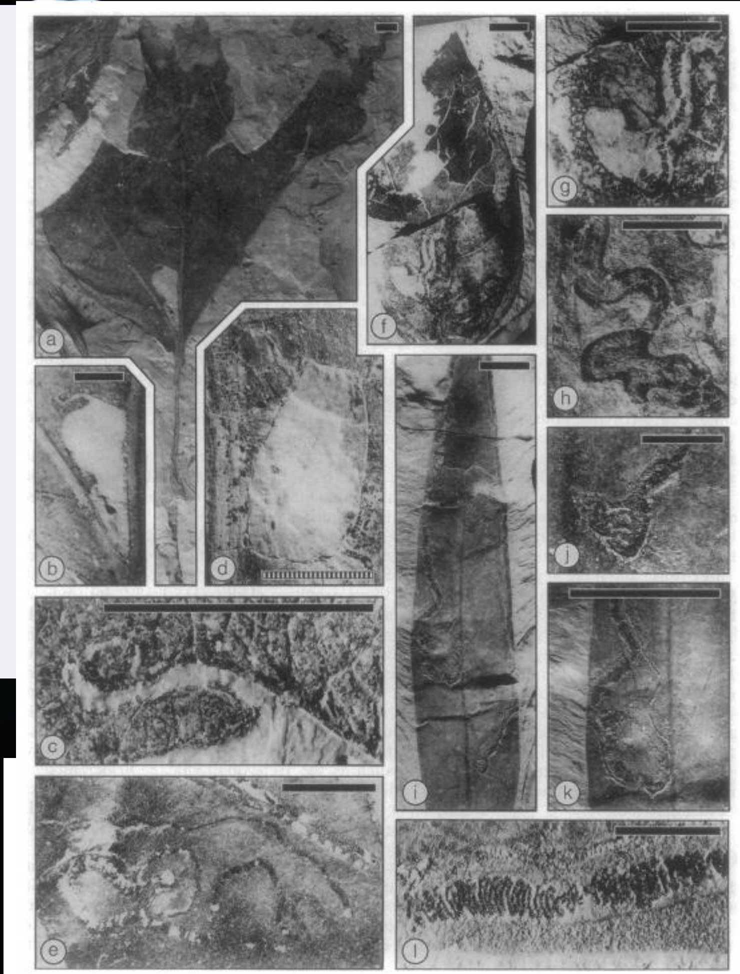
Mandibles are highly sclerotized to reduce wear

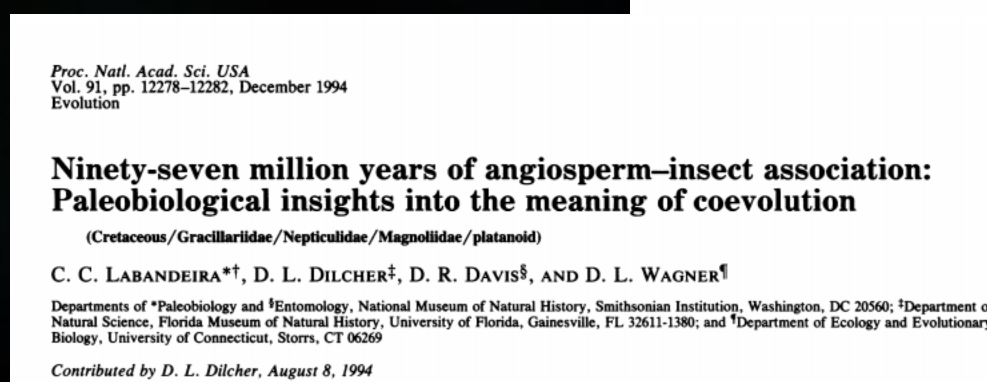
High silica content and cellulose can act as resistance to herbivory



Mining and Boring

- Insects live between the two epidermal layers of a leaf; damage appears as tunnels, blotches, or blisters
- Independently evolved in four orders: Diptera, Lepidoptera, Coleoptera and Hymenoptera
- Different species may excavate different layers of leaf parenchyma or reside in particular leaf parts





Proc. Natl. Acad. Sci. USA
Vol. 91, pp. 12278–12282, December 1994
Evolution

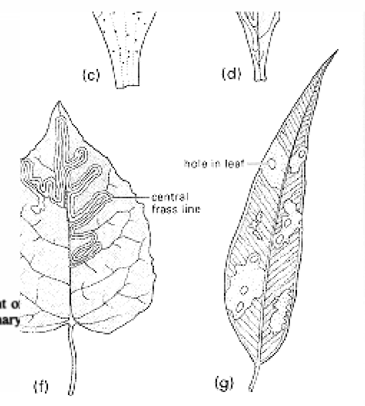
Ninety-seven million years of angiosperm–insect association: Paleobiological insights into the meaning of coevolution

(Cretaceous/Gracillariidae/Nepticulidae/Magnoliidae/platanoid)

C. C. Labandeira*†, D. L. Dilcher‡, D. R. Davis§, and D. L. Wagner¶

Departments of *Paleobiology and §Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560; ‡Department o[f] Natural Science, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611-1380; and ¶Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269

Contributed by D. L. Dilcher, August 8, 1994

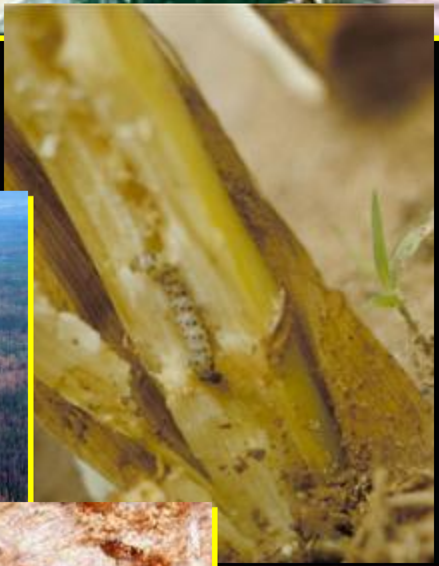


Mining and Boring

Stem mining
stem boring
plant boring
stalk boring
wood borers
fruit borers



Economically damaging


Types of Herbivory – Sap-sucking

Drain plant resources by tapping into xylem and phloem

Can retard growth and lead to overall lower biomass

Often transmit diseases

Hemipterans exemplify this strategy (haustellate mouthparts)

Fulgora laternaria

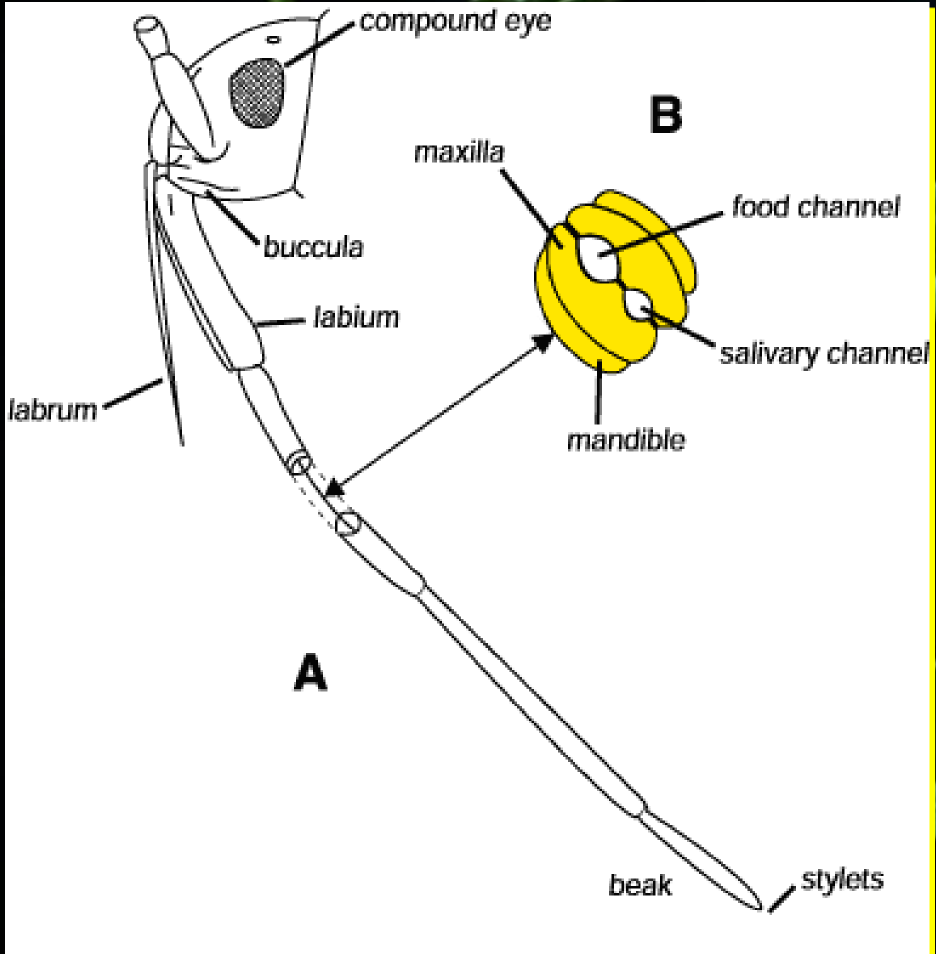
Types of Herbivory – Sap – sucking

Serve to pierce plant tissues and suck liquid food

Labium modified into a sheath
enclosing stylet maxillae

Stylets pierce cuticle and can
change orientation

Food channel empties
into cibarial cavity



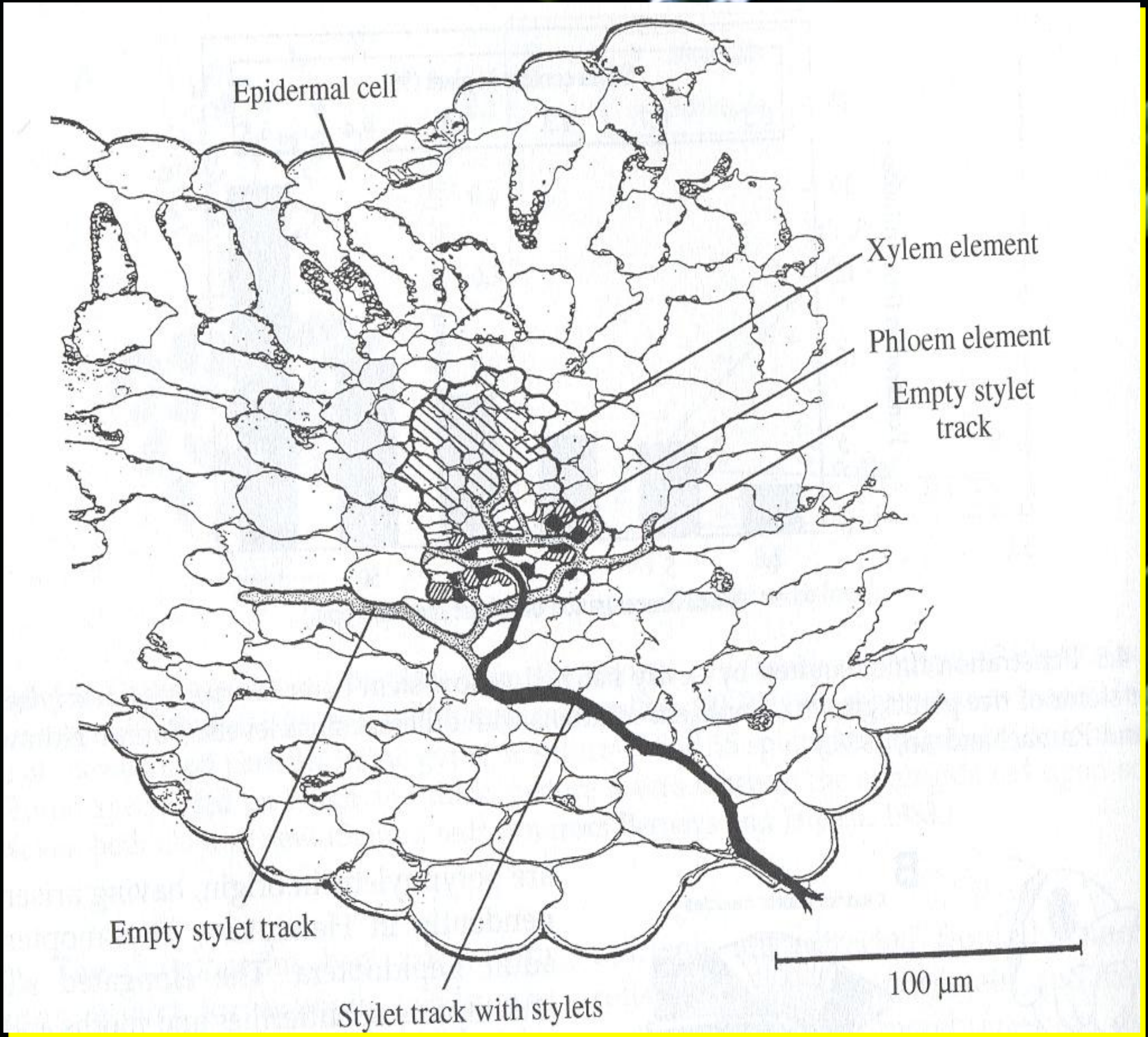
A, lateral view of the head showing beak, with the labrum detached from the front of beak

B, cross section of stylets

Stylet pathway is mostly extracellular

Locating suitable feeding site is a tedious task

Aphids ~4 hrs to find suitable phloem



Sucking insects utilize several kinds of plant fluids

Aphids, mealybugs, Cicadellidae, Psyllidae – Phloem cells

Sub order – Heteroptera and scale insects – Parenchyma

Many plants support both mandibulate and haustellate insect species

CHEWERS

No relative size restrictions

Heavy mechanical damage

Faced with indigestible compounds and toxins

SUCKERS

Restricted to a relatively small size

Avoid mechanical damage (but still damaging)

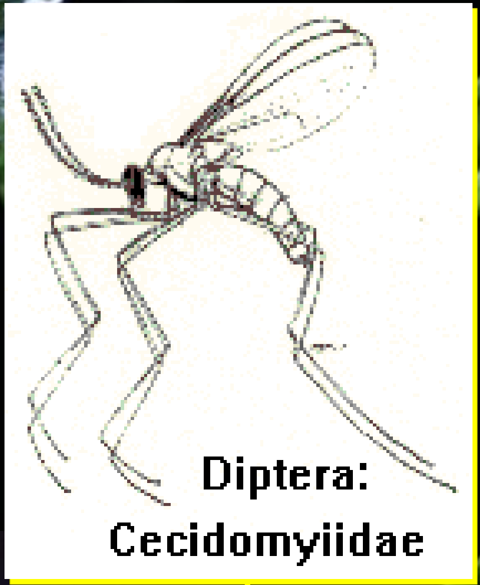
Avoid indigestible compounds and most toxins

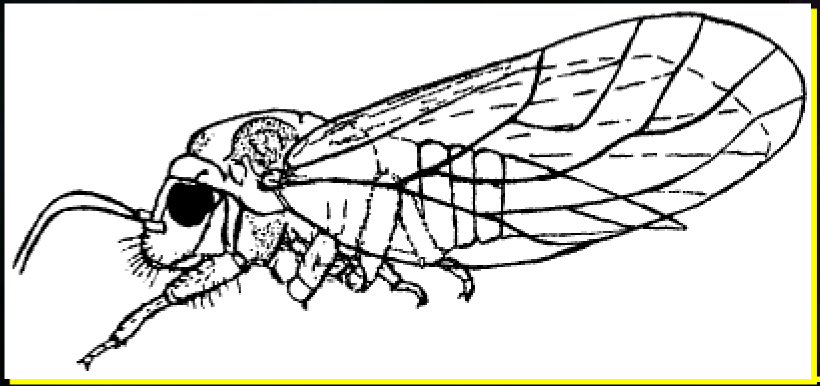
Xylem less suitable

Types of Herbivory – Gall makers

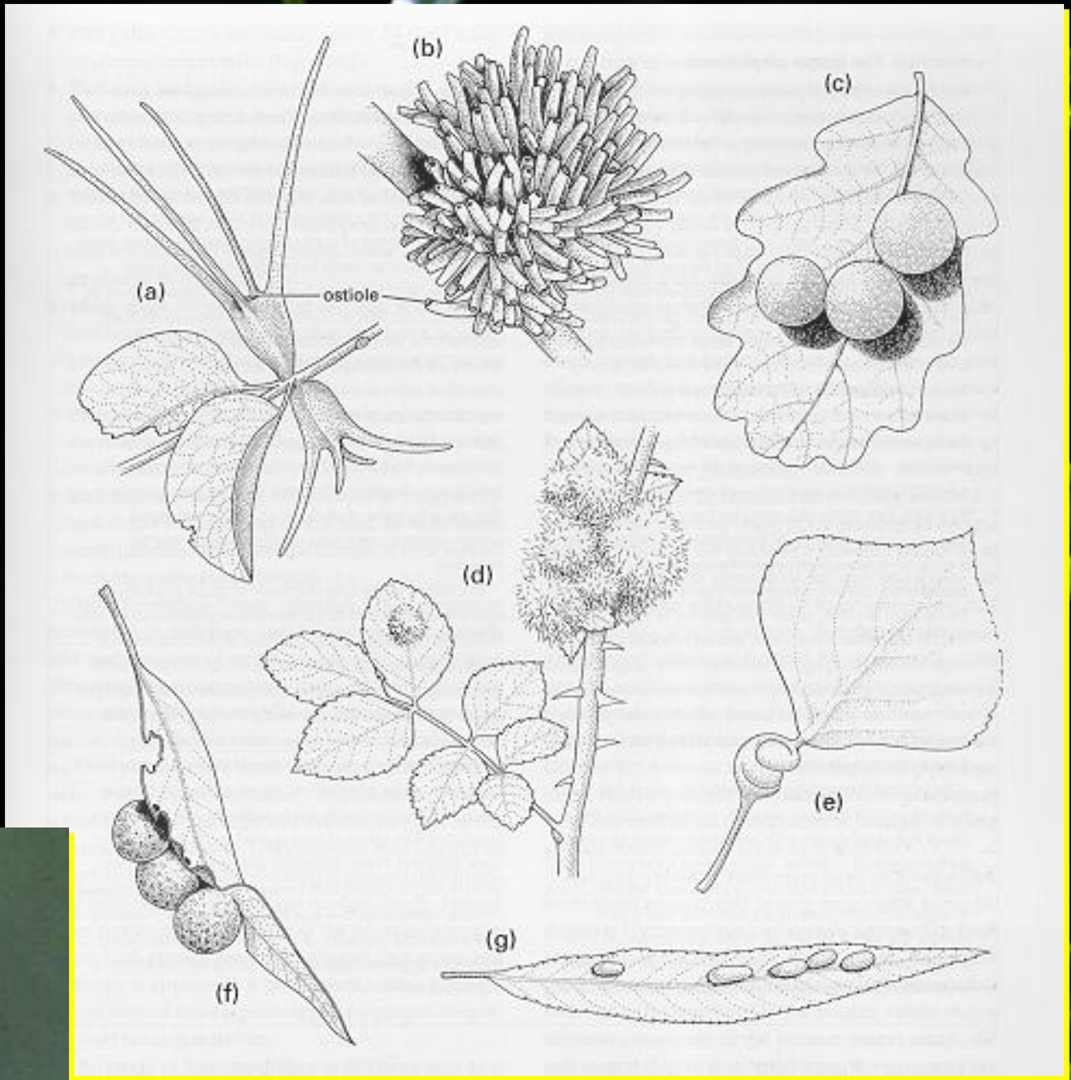
Galls consist of pathologically developed cells, tissues or organs of plants that have arisen by hypertrophy and/or hyperplasia as a result of stimulation from foreign organisms

Orders that make galls:
Hemiptera – Sternorryncha
Diptera – Cecidomyiidae, Tephritidae,
Hymenoptera – Cynipoidea





Covering-coccoids, cynipids
Filz-cynipids
Roll and fold-aphids
Pouch-psyllid
Mark-sawflys
Pit
Bud and Rosette



Galls may be **determinate** (distinct tissue layers) or **indeterminate** (undifferentiated masses of cells).

DEFINITIONS

Monophagous – Insects that in nature occur only on one or a few closely related plant species


Oligophagous
BARRA
LOVER'S
PIPER LOVER BLUES BAR
Polyphagous

Polyphagous

Ceroplastes sinensis
200 sp host plants
From >50 families

Table 2.3 Percentage of insect species within taxonomic groups that feed on plants within a single plant genus, or within a single plant family, or on more than one family of plants. Note that the first five groups of insects comprise small insects compared to the other groups. The correlation between size and host-plant range, however, is low. Many examples exist of closely related similarly-sized insects that show large differences in extent of host-plant ranges. NA=Data not available. (Source: modified from Mattson *et al.*, 1988)

	% of species feeding on			
Insect group	*One plant genus only*	*One plant family only*	*More than one plant family*	*No. of species*
Psyllidae	94	3	0	78
Aphidinae	91	7	2	445
Scolytidae	59	38	3	NA
Diaspididae	58	8	34	64
Thysanoptera	56	15	29	88
Nymphalidae	56	11	33	88
Lycaenidae	55	14	31	89
Pieridae	33	53	14	43
Papilionidae	25	21	54	89
Other Macrolepidoptera	17	23	60	430

COEVOLUTION

Ehrlich, P.R. and P.H. Raven, 1964. Butterflies and plants: a study in coevolution. Evolution 18:568-608.

•Many plant taxa manufacture novel secondary compounds that are mildly noxious.

•Some insect taxa feed on plants with the compounds and reduce plant fitness.

•Mutation/recombination introduce more toxic plant compounds.

•Insect feeding is reduced and toxicity in plants is selected for.

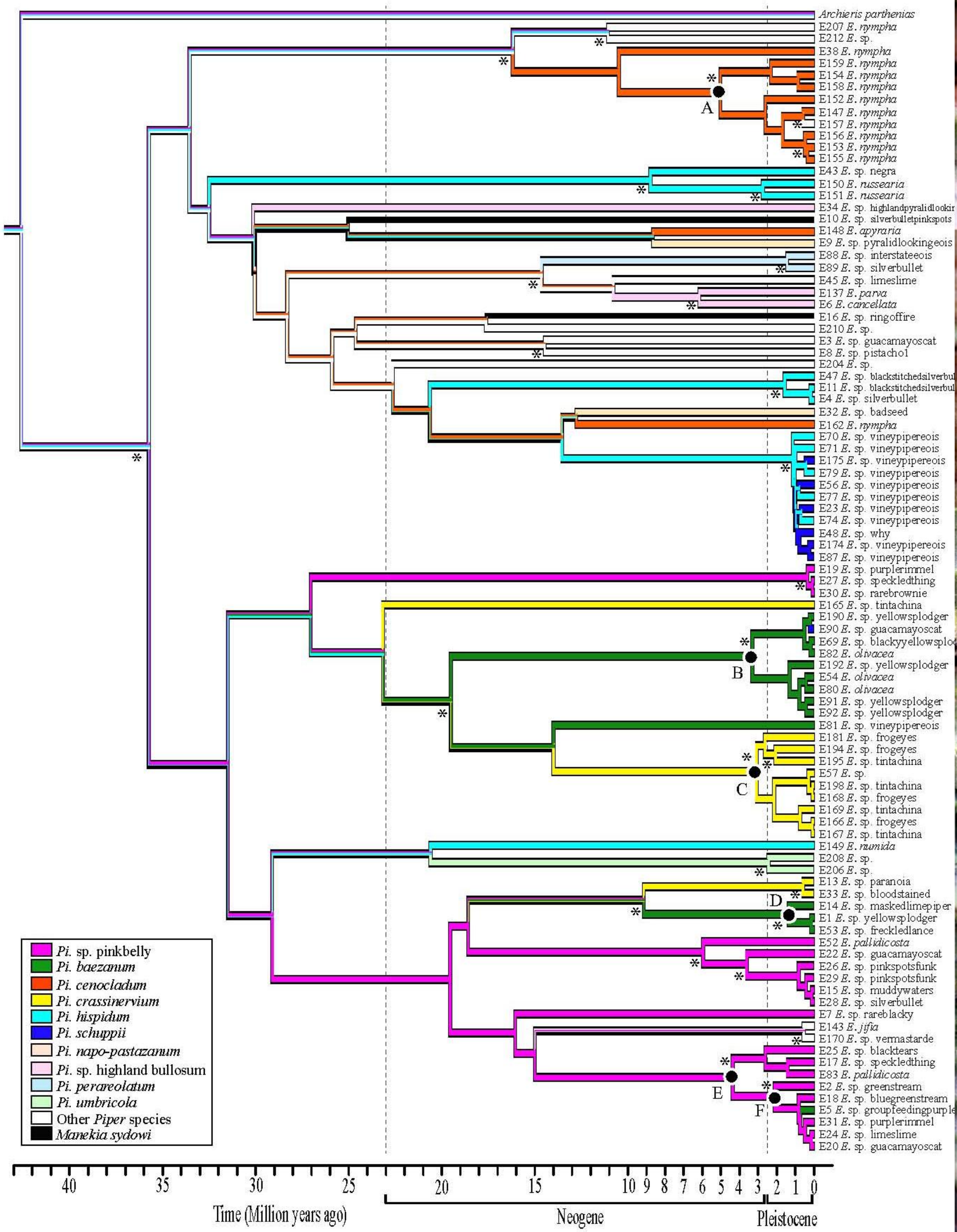
•The plant taxon goes through adaptive radiation.

•Insects evolve tolerance of or attraction to the novel compound and tend to specialize on plants with that toxin. The insect taxon goes through adaptive radiation.

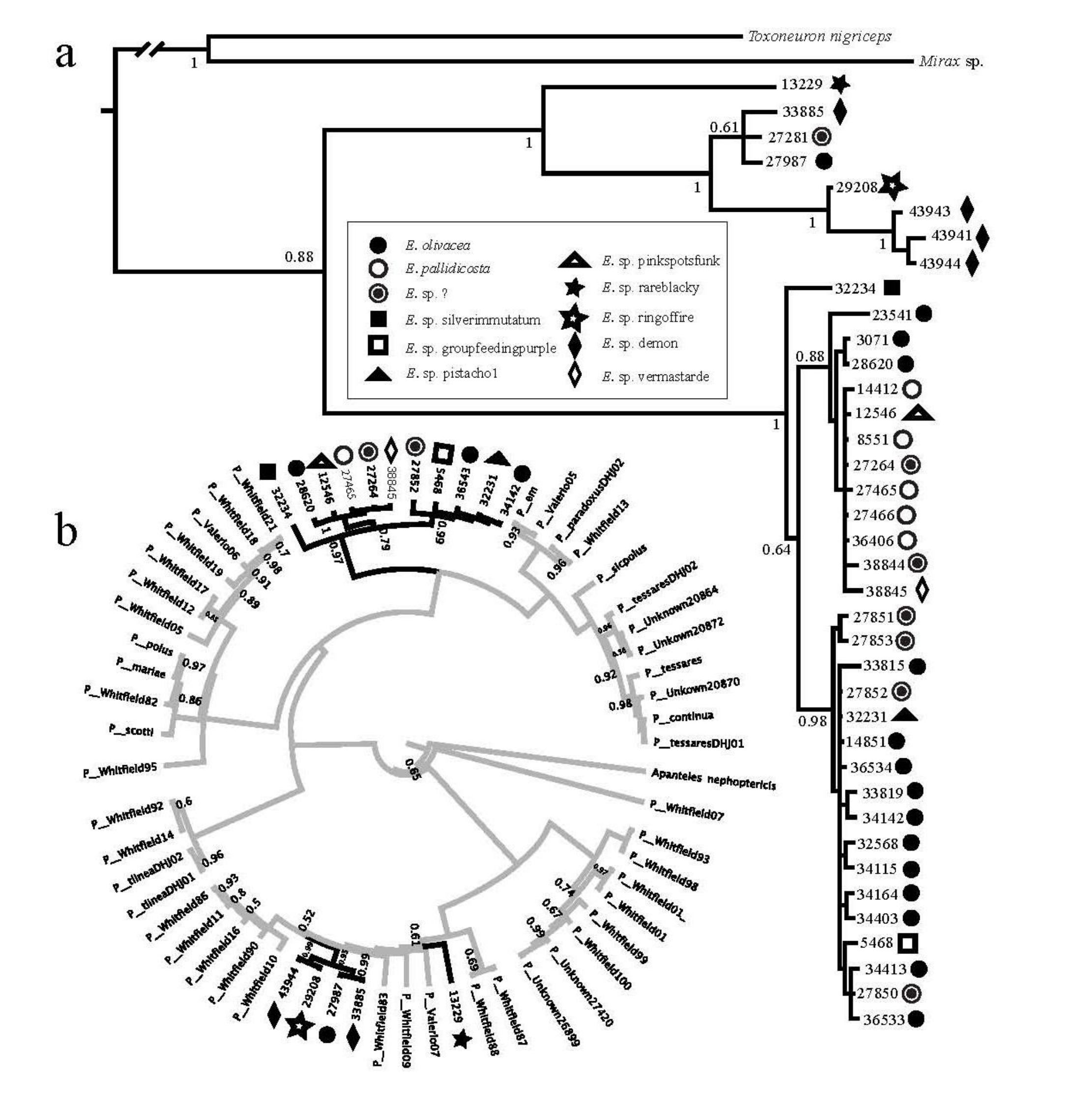
•The cycle is repeated, resulting in more phytochemicals and more feeding specialization.

Tritrophic view of specialization

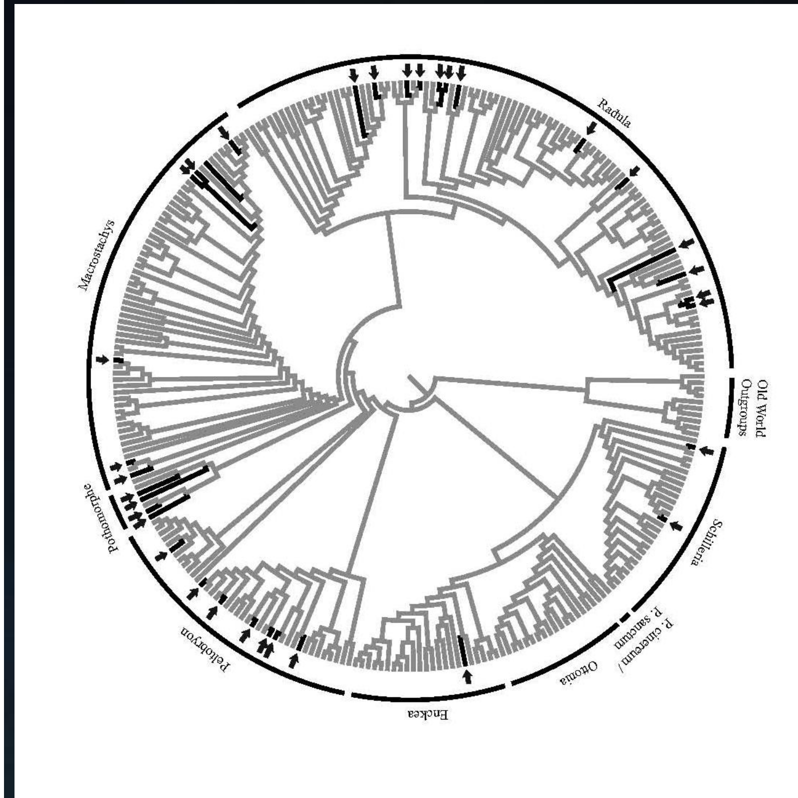
The top-down view holds that specialists are better able than generalists to utilize plant chemical or physical characteristics as defenses against enemies (Brower 1958, Atsatt 1981, Bernays 1988, Bernays and Cornelius 1989, Bernays and Graham 1988, Jones et al. 1989, Dyer and Floyd 1993, Dyer 1995).



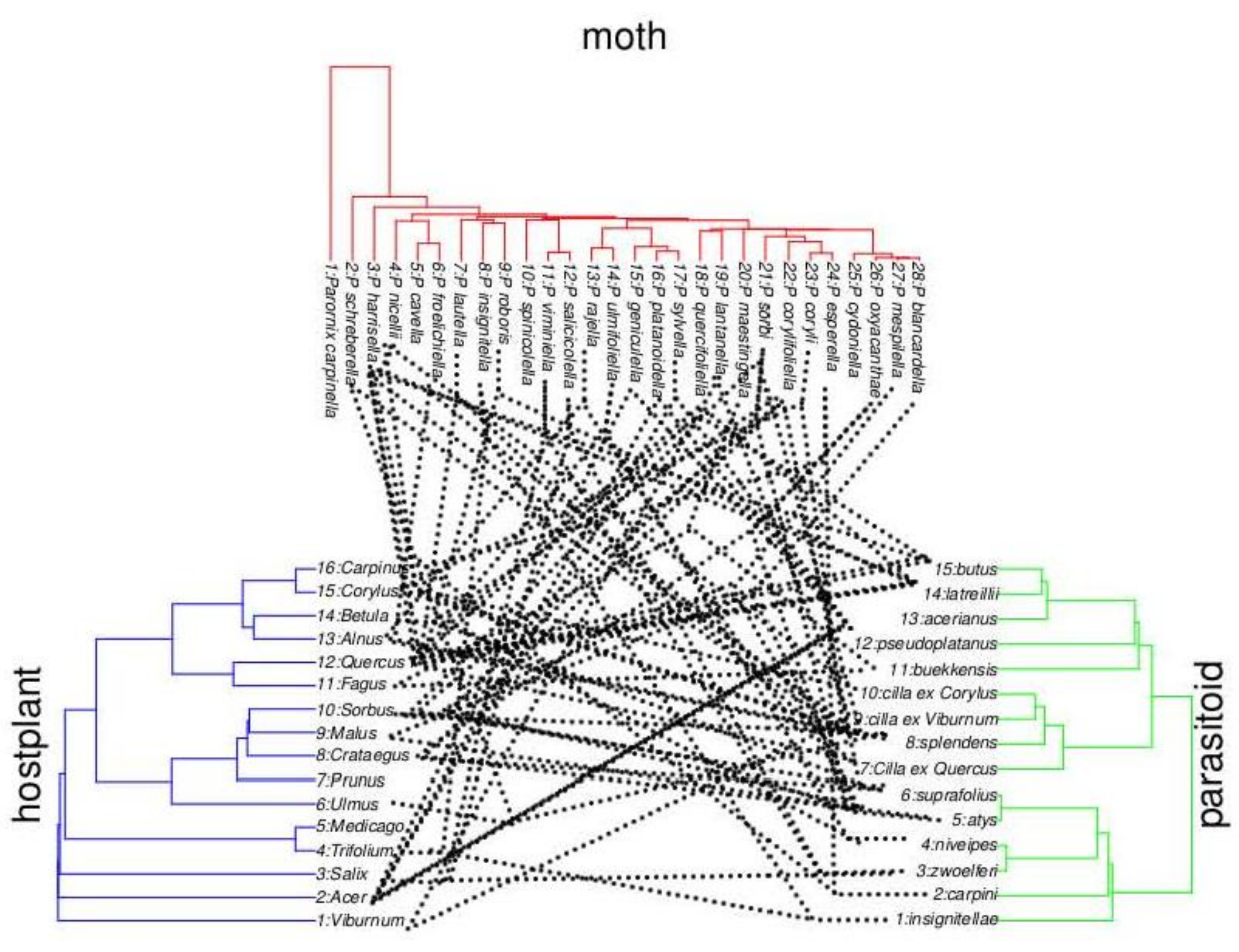
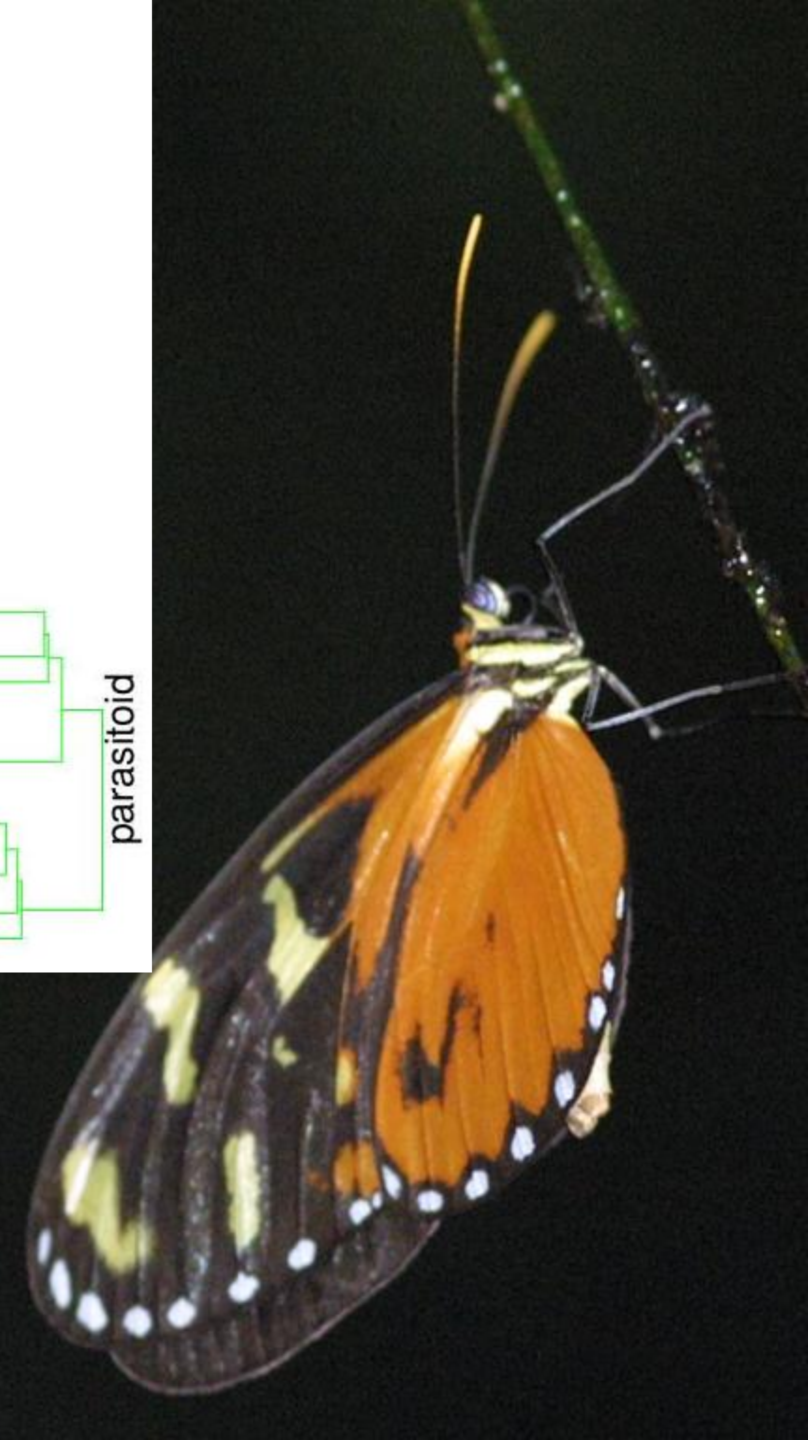
Wilson et al. Journal of Evolutionary Biology 2012



a
Toxoneuron nigriceps
Mirax sp.
E. olivacea
E. pallidicosta
E. sp. ?
E. sp. silverimmutatum
E. sp. groupfeedingpurple
E. sp. pistacho1
E. sp. pinkspotsfunk
E. sp. rareblacky
E. sp. ringoffire
E. sp. demon
E. sp. vermastarde
b
Apanteles nephoptericis

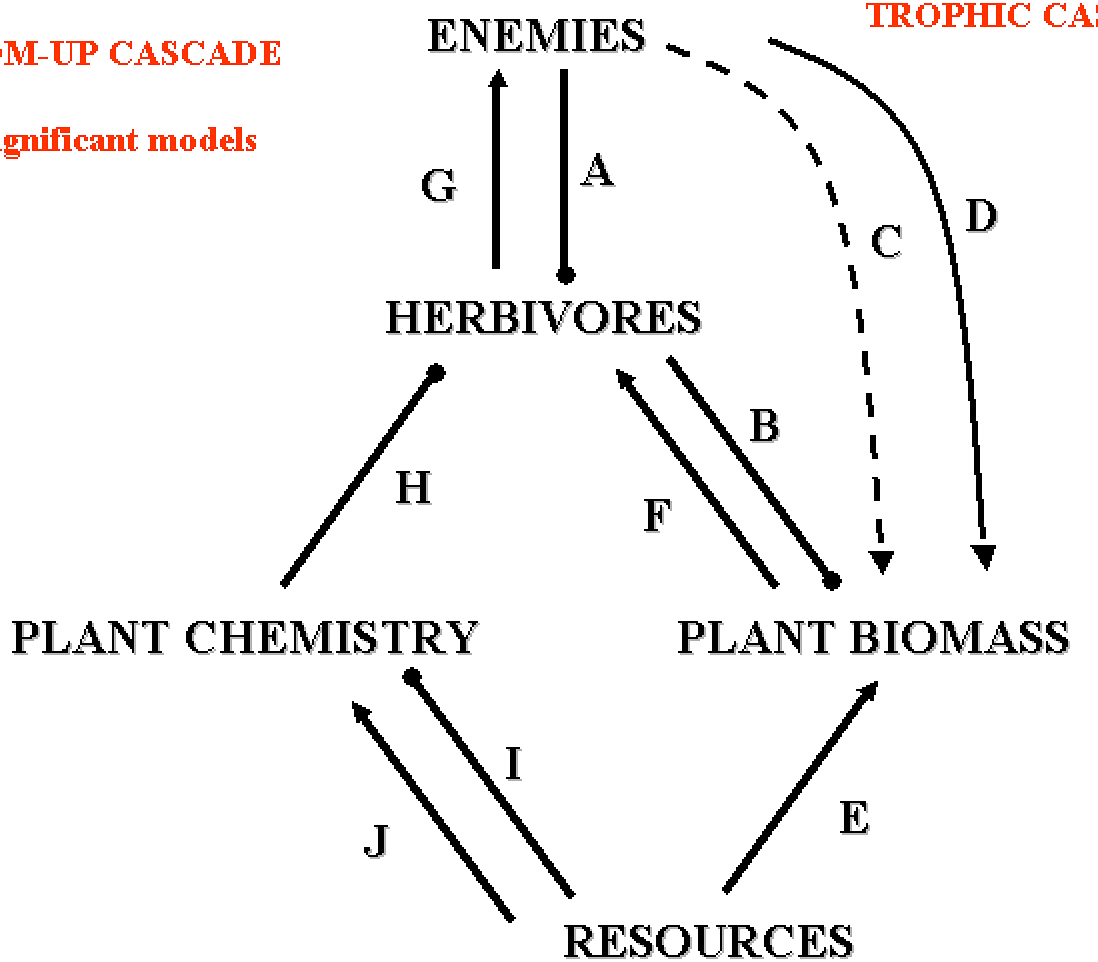


Radula
Macrostachys
Old World Outgroups
Schilleria
P. cinereum / P. sanctum
Ottonia
Enckea
Pelobryon
Pothomorphe


moth
1:Parornix carpinella
2:P schreberella
3:P harrisella
4:P nicellii
5:P cavella
6:P froelichiella
7:P lautella
8:P insignitella
9:P roboris
10:P spinicolella
11:P viminiella
12:P salicicolella
13:P rajella
14:P ulmifoliella
15:P geniculella
16:P platanoidella
17:P sylvella
18:P quercifoliella
19:P lantanella
20:P maestingella
21:P sorbi
22:P corylifoliella
23:P coryli
24:P esperella
25:P cydoniella
26:P oxyacanthae
27:P mespilella
28:P blancardella
hostplant
16:Carpinus
15:Corylus
14:Betula
13:Alnus
12:Quercus
11:Fagus
10:Sorbus
9:Malus
8:Crataegus
7:Prunus
6:Ulmus
5:Medicago
4:Trifolium
3:Salix
2:Acer
1:Viburnum
parasitoid
15:butus
14:latreillii
13:acerianus
12:pseudoplatanus
11:buekkensis
10:cilla ex Corylus
9:cilla ex Viburnum
8:splendens
7:Cilla ex Quercus
6:suprafolius
5:atys
4:niveipes
3:zwoelferi
2:carpini
1:insignitellae


HSS
BOTTOM-UP CASCADE
OFAN
Other significant models

TROPHIC CASCADES MODELS



Omnivory
IGP
Nonlinear trophic structure
Functional trophic levels
Donor, transmitter, receiver
Detrital food webs
Community-wide cascades

Troubles and enhancements....