

Episodes in history of the Hemiptera



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Diversity of insects



- Coleoptera – ca. 400.000 species, 204 families; 38%
- Lepidoptera – ca. 180.000 species, 126 families; 17%
- Hymenoptera – ca. 155.000 species, 132 families; 15%
- Diptera – ca. 125.000 species, 241 families; 12%
- Hemiptera – ca. 82.000 species **300 families**; 8%
- other insects – ca. 100.000 species; 10%



IUGS

INTERNATIONAL CHRONOSTRATIGRAPHIC CHART

www.stratigraphy.org

International Commission on Stratigraphy

v 2016/04



| Extinction Extinct Survived | Series / Epoch | Stage / Age | numerical age (Ma) |
|-----------------------------------|----------------|-------------|-----------------------|
| Phanerozoic | Cenozoic | Quaternary | Holocene |
| | | | Upper |
| | | | Middle |
| | | Pleistocene | Calabrian |
| | | | Gelasian |
| | | | Piacenzian |
| | | Pliocene | Zanclean |
| | | | Messinian |
| | | | Tortonian |
| | | Neogene | Serravallian |
| | | | Langhian |
| | | | Burdigalian |
| | | | Aquitanian |
| | | | Chattian |
| | | | Rupelian |
| | | | Oligocene |
| | Paleogene | Eocene | Priabonian |
| | | | Bartonian |
| | | | Lutetian |
| | | | Ypresian |
| | | | Thanetian |
| | | Paleocene | Selandian |
| | | | Danian |
| | | | Maastrichtian |
| | | Upper | Campanian |
| | | | Santonian |
| | | | Coniacian |
| | | | Turonian |
| | | | Cenomanian |
| | | | Albian |
| | | | Aptian |
| Mesozoic | Cretaceous | Lower | Barremian |
| | | | Hauterivian |
| | | | Valanginian |
| | | | Berriasian |
| | | | |
| | | | |

| Extinction Extinct Survived | Series / Epoch | Stage / Age | numerical age (Ma) |
|-----------------------------------|----------------|-------------|-----------------------|
| Phanerozoic | Mesozoic | Jurassic | Tithonian |
| | | | Kimmeridgian |
| | | | Oxfordian |
| | | | Callovian |
| | | | Bathonian |
| | | Middle | Bajocian |
| | | | Aalenian |
| | | | Toarcian |
| | | Lower | Pliensbachian |
| | | | Sinemurian |
| | | | Hettangian |
| | | | Rhaetian |
| | | | Norian |
| | | | Carnian |
| | Triassic | Upper | Ladinian |
| | | | Anisian |
| | | Middle | Olenekian |
| | | | Induan |
| | | | Changhsingian |
| | Paleozoic | Permian | Wuchiapingian |
| | | | Capitanian |
| | | | Wordian |
| | | | Roadian |
| | | | Kungurian |
| | | Cisuralian | Artinskian |
| | | | Sakmarian |
| | | | Asselian |
| | | | Gzhelian |
| | | | Kasimovian |
| Carboniferous | Pennsylvanian | Upper | Bashkirian |
| | | | Moscovian |
| | | | Serpukhovian |
| | | Middle | Visean |
| | | | Tournaisian |
| | Mississippian | Lower | |
| | | | |
| | | | |
| | | | |
| | | | |

| Extinction Extinct Survived | Series / Epoch | Stage / Age | numerical age (Ma) |
|-----------------------------------|----------------|-------------|-----------------------|
| Phanerozoic | Paleozoic | Devonian | Famennian |
| | | | Frasnian |
| | | | Givetian |
| | | | Eifelian |
| | | | Emsian |
| | | Middle | Pragian |
| | | | Lochkovian |
| | | | Pridoli |
| | | Silurian | Ludlow |
| | | | Ludfordian |
| | | | Gorstian |
| | | | Homerian |
| | | | Sheinwoodian |
| | Ordovician | Upper | Telychian |
| | | | Aeronian |
| | | | Rhuddanian |
| | | | Hirnantian |
| | | | Katian |
| | | Middle | Sandbian |
| | | | Darriwilian |
| | | | Dapingian |
| | | Lower | Floian |
| | | | Tremadocian |
| Cambrian | Furongian | Series 10 | Stage 10 |
| | | | Jiangshanian |
| | | | Paibian |
| | | | Guzhangian |
| | | | Drumian |
| | Series 3 | Stage 5 | Stage 5 |
| | | | Stage 4 |
| | | | Stage 3 |
| | | | Stage 2 |
| | | | Fortunian |

| Eonothem / Eon | Erathem / Era | System / Period | numerical age (Ma) |
|-------------------|-------------------|-----------------|-----------------------|
| Proterozoic | Neo-proterozoic | Ediacaran | 541.0 ± 1.0 |
| | | Cryogenian | ~ 635 |
| | | Tonian | ~ 720 |
| | Meso-proterozoic | Stenian | 1000 |
| | | Ectasian | 1200 |
| | | Calymnian | 1400 |
| | Paleo-proterozoic | Statherian | 1600 |
| | | Orosirian | 1800 |
| | | Rhyacian | 2050 |
| | | Siderian | 2300 |
| | | | 2500 |
| Archean | Neo-archean | | 2800 |
| | | | 3200 |
| | Meso-archean | | 3600 |
| | | | 4000 |
| | Eo-archean | | ~ 4600 |
| Hadean | | | |

Units of all ranks are in the process of being defined by Global Boundary Stratotype Section and Points (GSSP) for their lower boundaries, including those of the Archean and Proterozoic, long defined by Global Standard Stratigraphic Ages (GSSA). Charts and detailed information on ratified GSSPs are available at the website <http://www.stratigraphy.org>. The URL to this chart is found below.

Numerical ages are subject to revision and do not define units in the Phanerozoic and the Ediacaran; only GSSPs do. For boundaries in the Phanerozoic without ratified GSSPs or without constrained numerical ages, an approximate numerical age (–) is provided.

Numerical ages for all systems except Lower Pleistocene, Permian, Triassic, Cretaceous and Precambrian are taken from 'A Geologic Time Scale 2012' by Gradstein et al. (2012); those for the Lower Pleistocene, Permian, Triassic and Cretaceous were provided by the relevant ICS subcommissions.

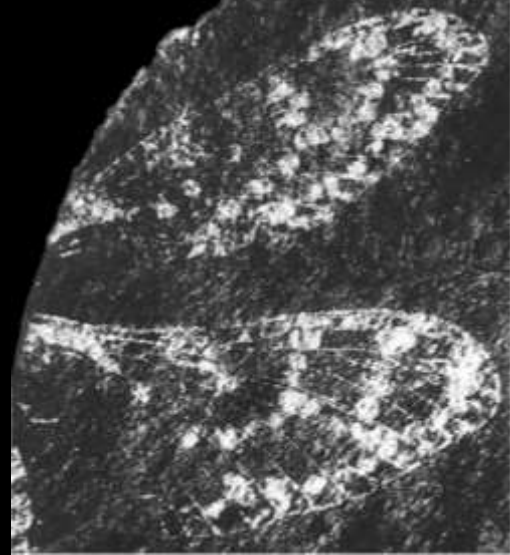
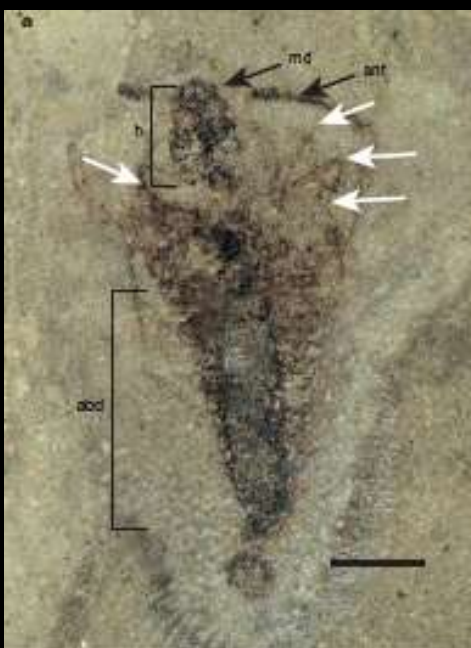
Coloring follows the Commission for the Geological Map of the World (<http://www.ccgw.org>)

Chart drafted by K.M. Cohen, S.C. Finney, P.L. Gibbard
(c) International Commission on Stratigraphy, April 2016

To cite: Cohen, K.M., Finney, S.C., Gibbard, P.L. & Fan, J.-X. (2013; updated)
The ICS International Chronostratigraphic Chart. Episodes 36: 199-204.

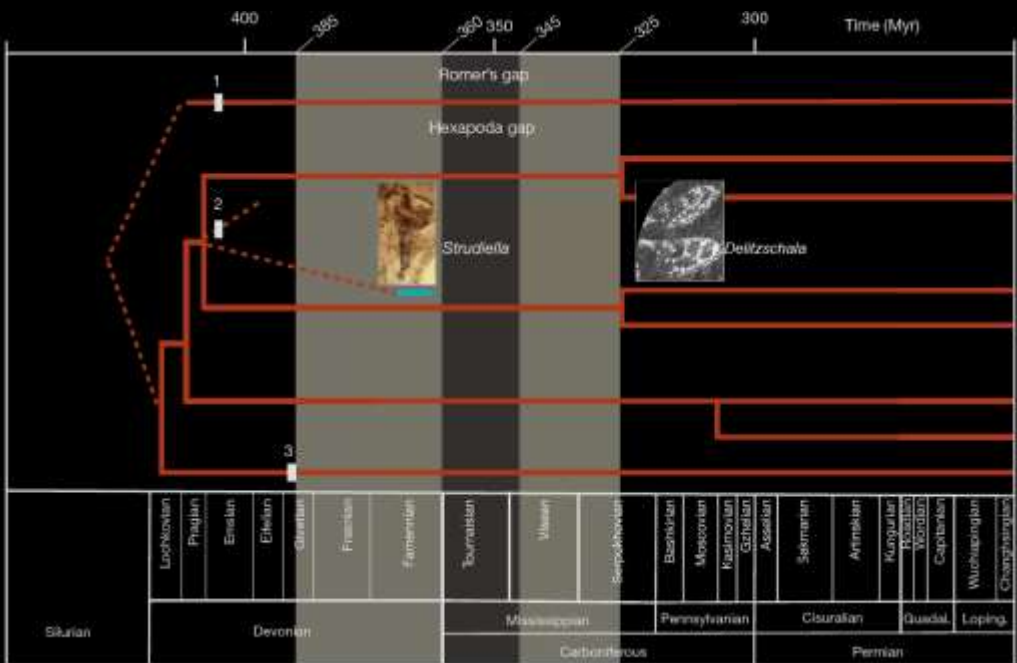
URL: <http://www.stratigraphy.org/ICSchart/ChronostratChart2016-04.pdf>





Strudiella devonica Garrouste *et al.*, 2012
Fammenian, Devonian; Strud, Namur, Belgium

Delitzschala bitterfeldensis
Brauckmann et Schneider, 1996
Arnsbergian (Namurian A),
Late Mississippian, Germany



System and classification:

Ordo: Hemiptera Linnaeus, 1758

Subordines: †Paleorrhyncha Carpenter, 1931

Sternorrhyncha Duméril, 1806

Fulgoromorpha Evans, 1946

Cicadomorpha Evans, 1946

Coleorrhyncha Myers et China, 1929

Heteroptera Latreille, 1810

300 families known (recently 178 present),

the highest number among the insects!



CAROLI LINNÆI

EQUITIS DE STELLA POLARI,
ARCHIATRI REGII, MED. & BOTAN. PROFESS. UPSAL.;
ACAD. UPSAL. HOLMENS. PETROPOL. BEROL. IMPER.
LOND. MONSPEL. TOLOS. FLORENT. SOC.

SYSTEMA NATURÆ

PER
REGNA TRIA NATURÆ,

SECUNDUM
CLASSES, ORDINES,
GENERA, SPECIES,

CUM
CHARACTERIBUS, DIFFERENTIIS,
SYNONYMIS, LOCIS.

TOMUS I.

EDITIO DECIMA, REFORMATA.

Cum Privilegio S:æ R:æ M:tis Sveciæ.

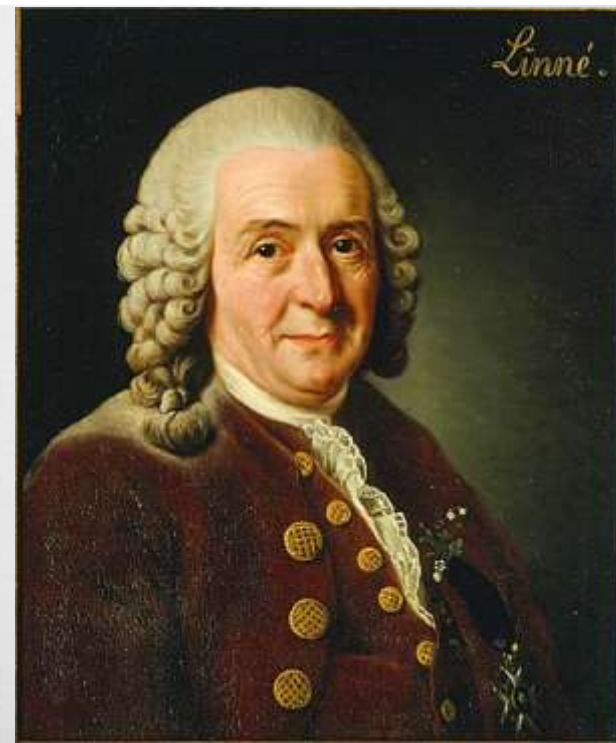
HOLMIÆ,
IMPENSIS DIRECT. LAURENTII SALVII,
1758.

INSECTA.

343

II. HEMIPTERA.

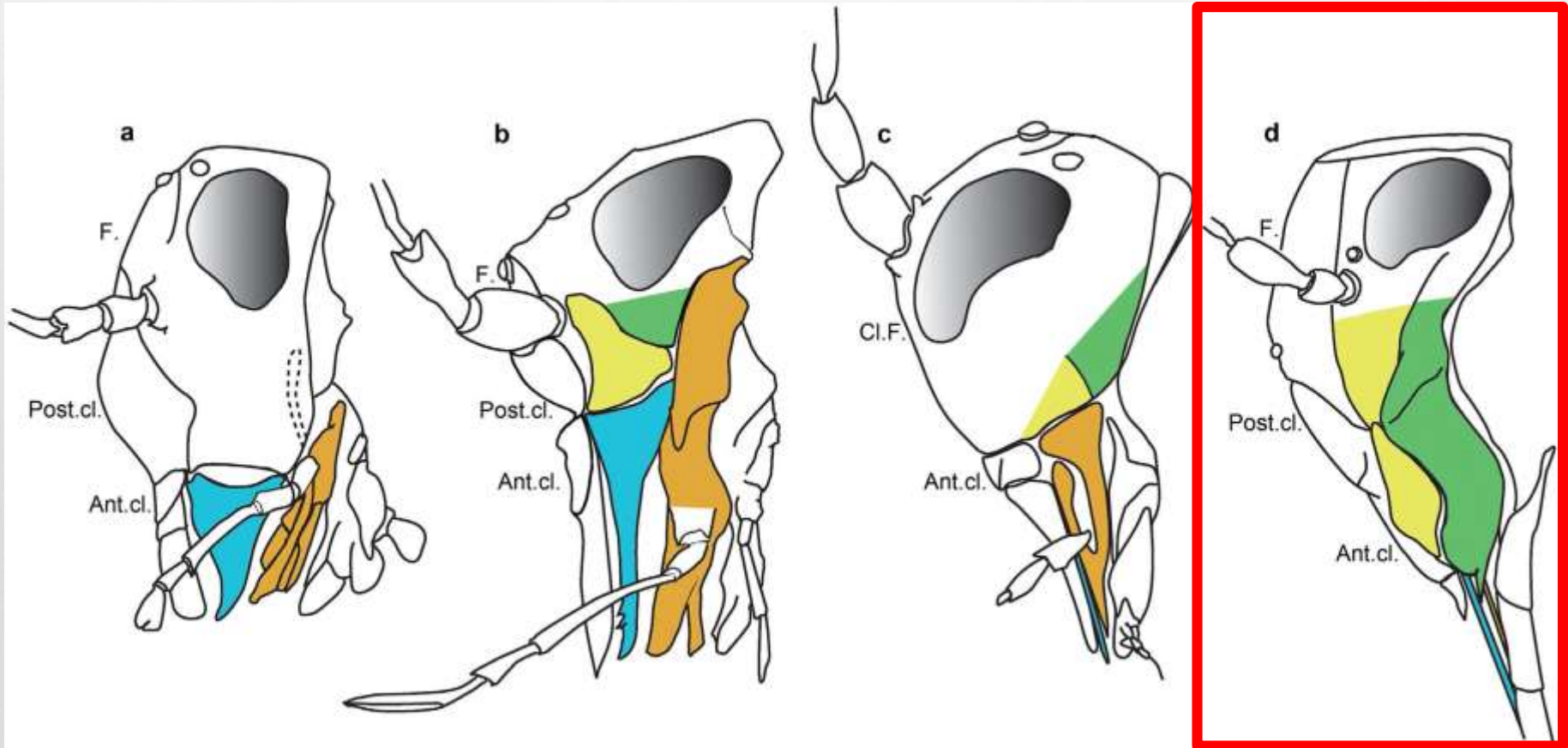
195. CICADA *Rostrum* inflexum. *Pedes* postici saltatorii.
196. NOTONECTA *Rostrum* inflexum. *Pedes* postici natatorii
(ciliati.)
197. NEPA *Rostrum* inflexum. *Pedes* antici capitis cheliferi.
198. CIMEX *Rostrum* inflexum. *Pedes* cursorii.
199. APHIS *Rostrum* inflexum. *Abdomen* bicornæ.
200. CHERMES *Rostrum* pectorale. *Pedes* postici saltatorii.
201. COCCUS *Rostrum* pectorale. *Abdomen* postice setosum maribus.
202. THRIPS *Rostrum* obsoletum. *Ala* incumbentes abdomini reflexi.



Hemiptera (Thripida included) – paraphyletic unit

Hypothesis of head and mouthpart morphologies in Acercaria (Paraneoptera)

(Huang *et al.* 2016)



(a) Psocodean groundpattern (also present in Hypoperlidae). (b) Permopsocidan groundpattern. (c) Thripidan groundpattern, reconstructed after the head of an adult Tubulifera, and Moundthrips. (d) Hemipteran groundpattern. Mandible: blue; maxilla: brown; anterior part of gena (mandibular lobe): yellow; posterior part of gena (maxillary lobe?): green. Ant.cl. anteclypeus; Cl.F. clypeo-frons; F. frons; Post.cl. postclypeus.

Synapomorphies of the Hemiptera:

- ❖ mouthparts developed into suctorial beak, with two pairs of mandibular and maxillary stylets lying in a long, grooved labium;
- ❖ maxillary and labial palps lost;
- ❖ ocelli close to compound eyes, median ocellus near postclypeus;
- ❖ veins ScP+R+M+CuA fused at base as common stem; transverse veinlet *cua-cup* developed in various degree
- ❖ vein ScP fused with RA, vein MA completely fused with vein RP;
- ❖ tarsi 3-segmented;
- ❖ cerci reduced;
- ❖ primarily, nymphs oval, flattened dorsoventrally, with short legs;
- ❖ chitin-protein peritrophic membrane lost replaced by lipoprotein perimicrovillar membrane

Possible synapomorphies (modern forms):

- ❖ hind legs jumping, hind tibia with apical rows formed by teeth provided with setae; first two tarsomeres enlarged;



Psocodea

Phthiraptera

HYPOPERLIDA

other Psocoptera

Liposcelidae

AMBLYCERA

ISCHNOCERA

RHYNCOPTHIRINA

ANOPLURA

PERMOPSOCIDA

THRIPIDA

PALEORRHYNCHA

STERNORRHYNCHA

FULGOROMORPHA

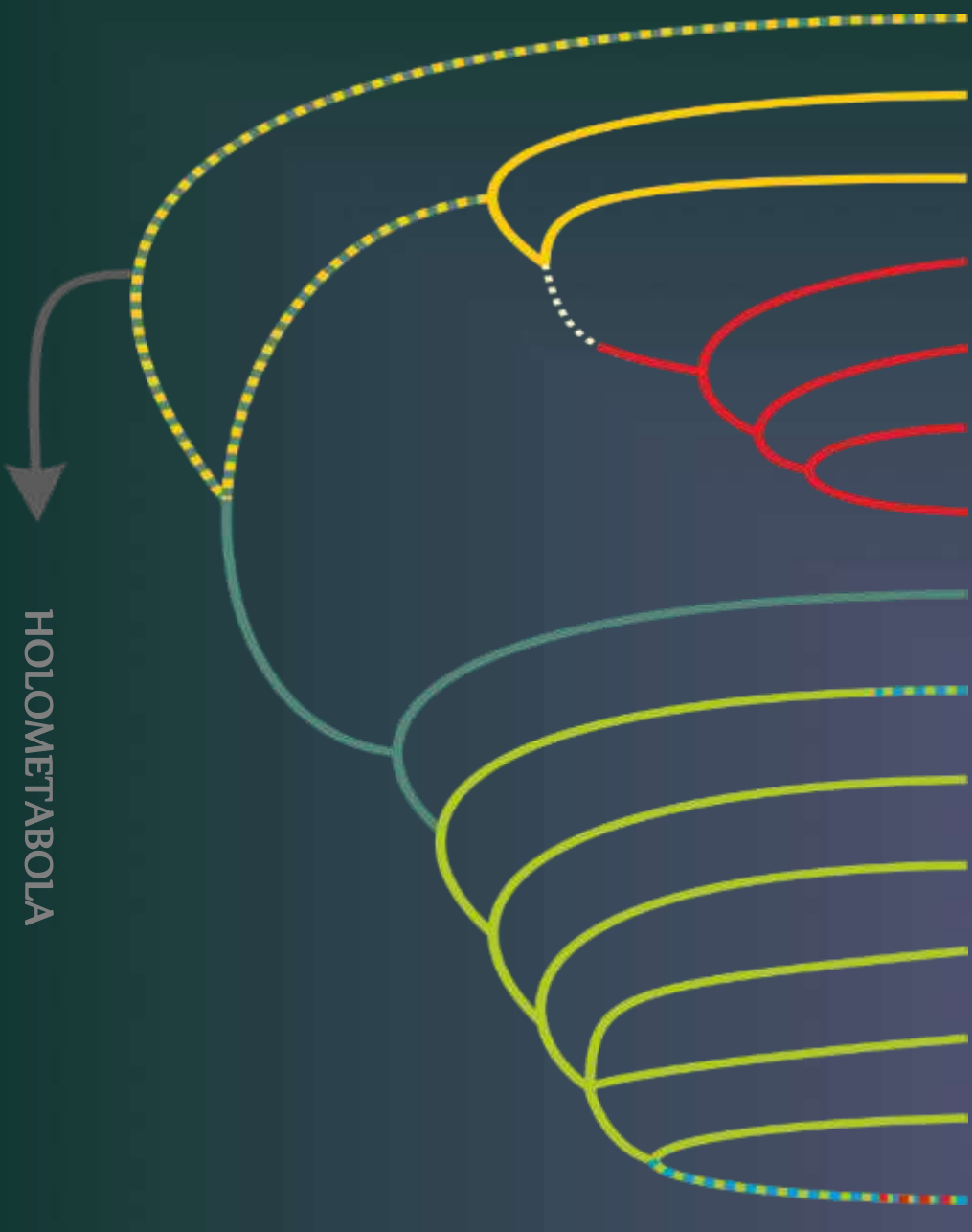
CICADOMORPHA

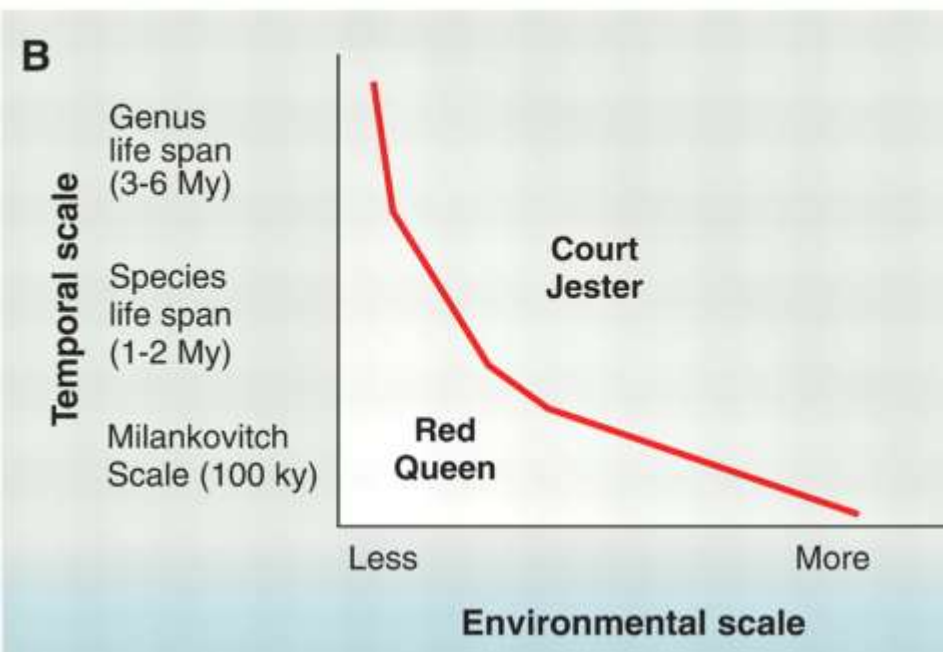
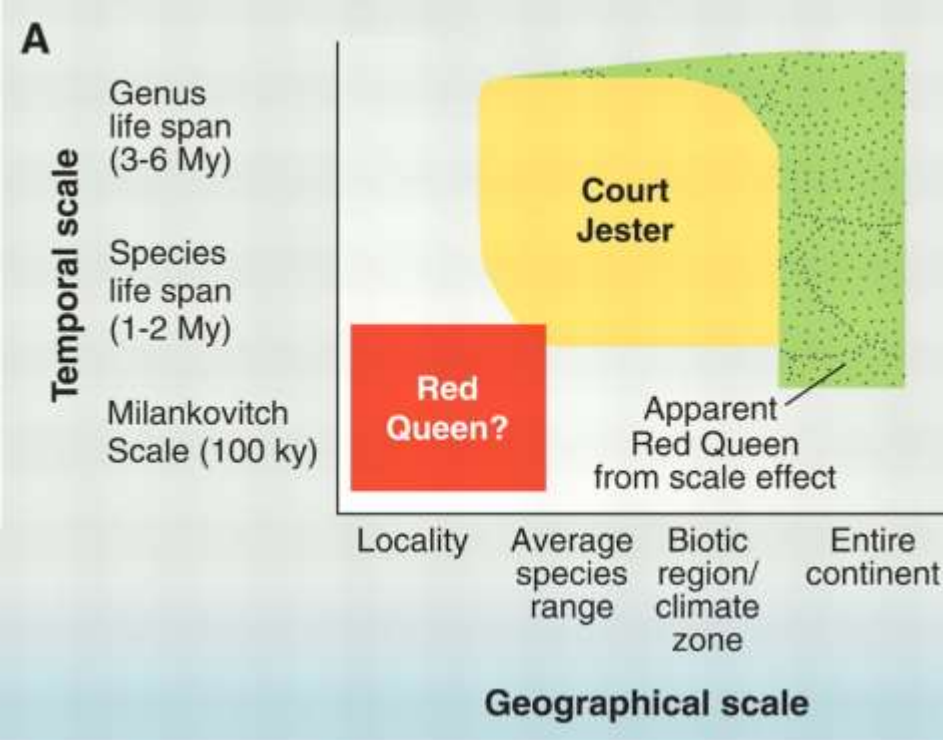
COLEORRHYNCHA

HETEROPTERA

Hemiptera

HOLOMETABOLA





Generally speaking, evolutionary processes may be dominated by biotic factors, as in the **Red Queen** model, or abiotic factors, as in the **Court Jester** model, or a mixture of both. These two models appear to operate predominantly over different geographic and temporal scales: competition, predation, parasitism and other biotic factors shape ecosystems locally and over short time spans, but extrinsic factors such as climate and tectonic events shape larger-scale patterns regionally and globally, and through thousands and millions of years. The current studies suggest that Hemiptera evolution is driven largely by abiotic factors such as climate, landscape, but biotic factors as food supply or new niches occupation are important factors for lineages formation. Comparative phylogenetic approach offer new insights into Hemiptera clade dynamics.

“It takes all the running you can do, to keep in the same place.”

The Red Queen, *Through the Looking-Glass*, Lewis Carroll.

“I believe whatever doesn’t kill you, simply makes you.... **stranger**.”

Joker, *The Dark Knight*, Christopher Nolan.



The **Red Queen** hypothesis was originally used to describe competition between species being the driving factor behind the large number of species we see today.

Another hypothesis, known as the **Court Jester** hypothesis suggests that changes in species may result not due to competition between species, but due to random geological or climate events that act as the driving force behind evolution, and the formation of new species.

... another player in the game of the Hemiptera evolution is involved –

The Red King.

Co-evolution of two partners is regarded usually as the factor

increasing the speed of evolutionary process, to avoid the run of **Red**

Queen.

Contrary, when two partners are tightly bond in mutualistic

relationship, the **Red King** effect may appear, i.e. the slowly evolving

species is likely to gain a disproportionate share of the benefits.

Moreover, population structure serves to magnify the advantage to the

slower species.



Episode 1



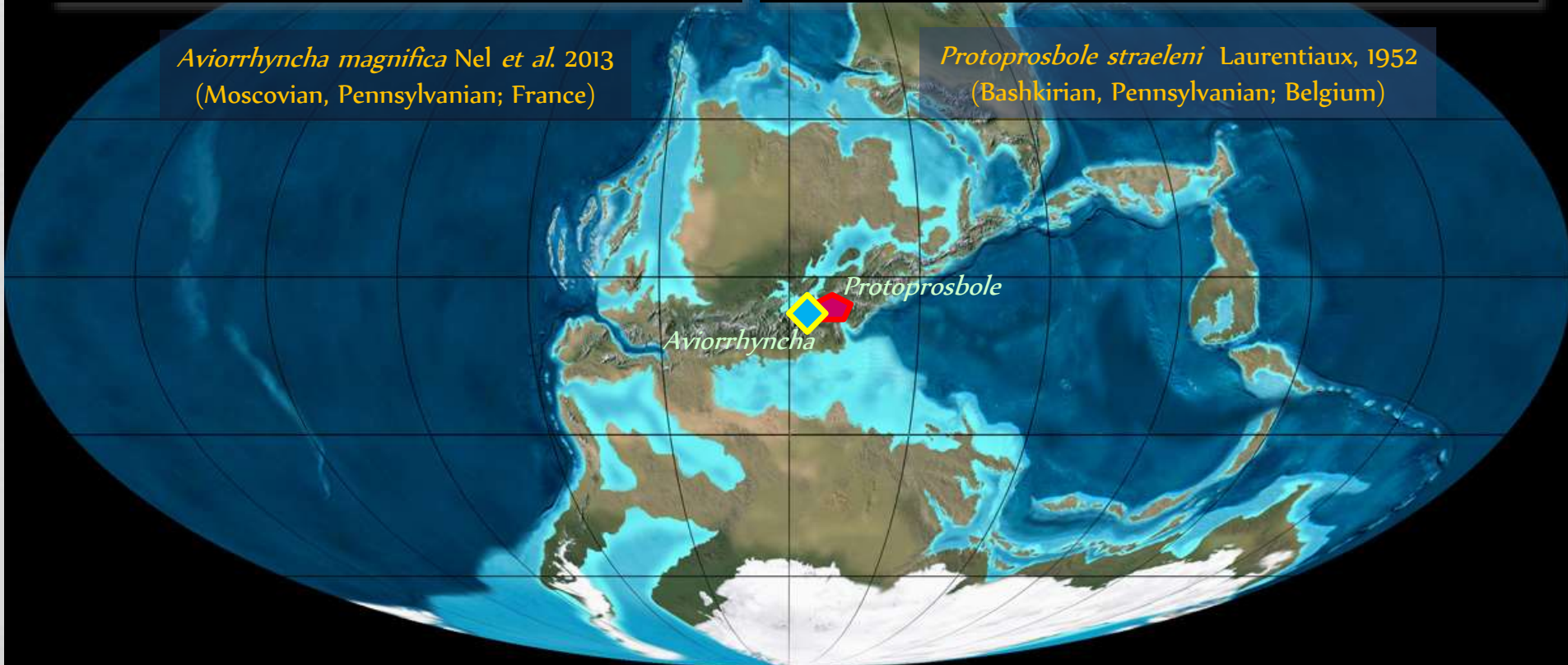
ORIGINS

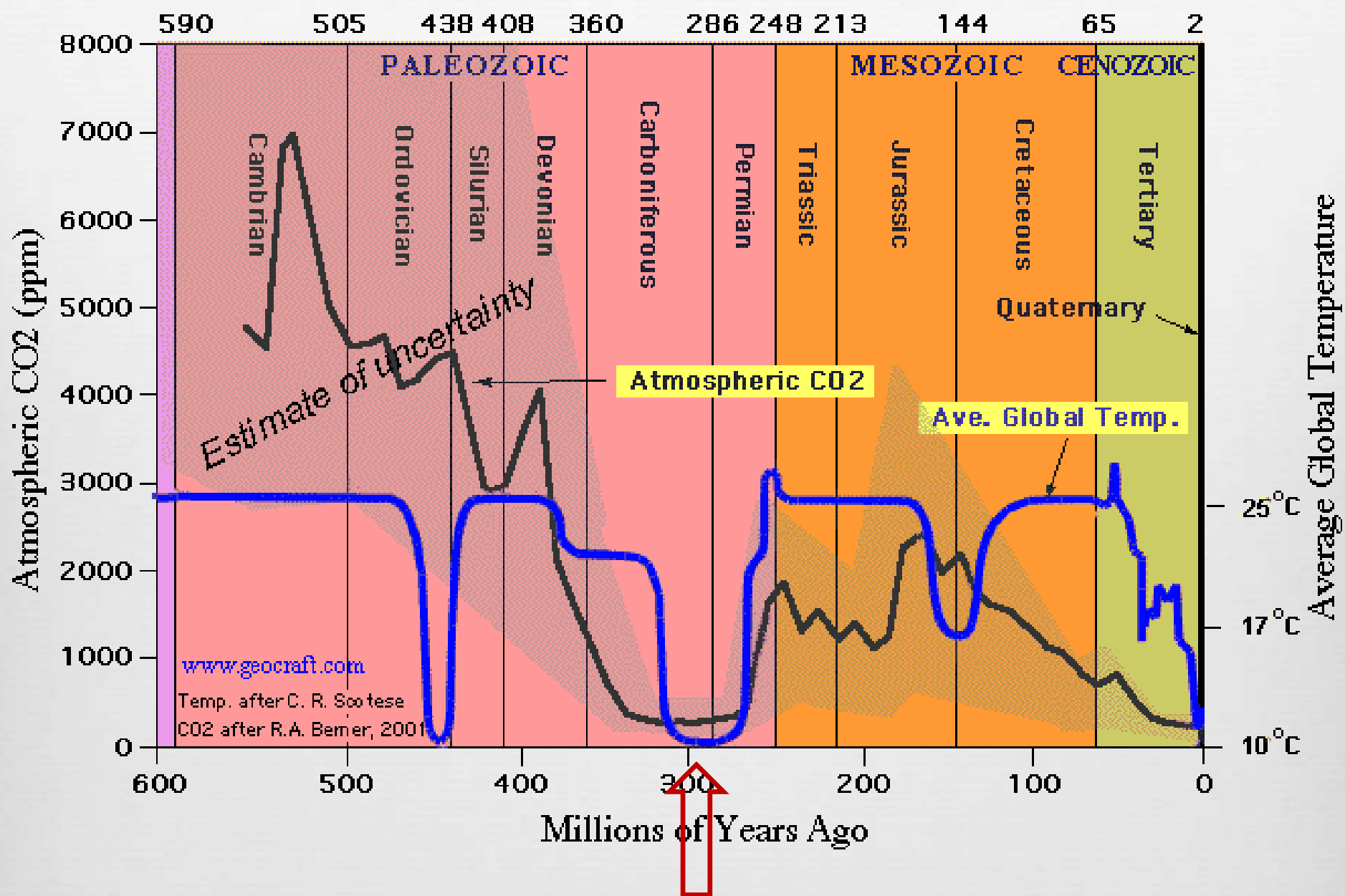


Aviorrhyncha magna Nel *et al.* 2013
(Moscovian, Pennsylvanian; France)



Protoprosbole straeleni Laurentiaux, 1952
(Bashkirian, Pennsylvanian; Belgium)





Do global cooling and atmosphere composition changes triggered diversification of the Hemiptera?

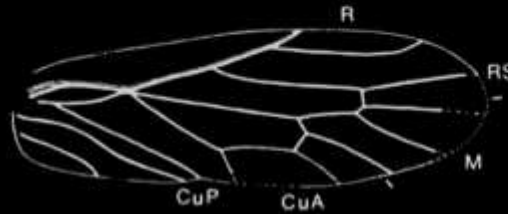
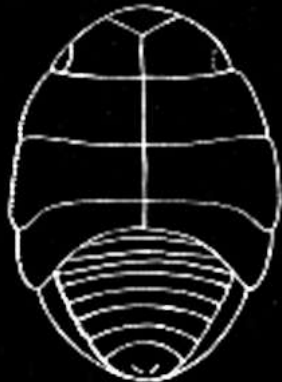
The Permian diversification

- ◆ Palaeorrhyncha – paraphyletic assemblage of ‘Archescytinidae’
 - ◆ earliest Sternorrhyncha – Pincombeomorpha, earliest Aphidomorpha
 - ◆ rapid and immense diversification of Cicadomorpha
 - ◆ earliest (but specialized) Fulgoromorpha – a few only
 - ◆ earliest Coleorrhyncha - Progonocimicidae
 - ◆ no record of the Heteroptera
-
- ◆ first endosymbiotic relationships very probable, but not necessarily the bacteria and yeasts we know in recent lineages
 - ◆ all these groups supposedly were phloem-feeders
 - ◆ open questions of biochemistry and physiology of Permian seed-ferns, early gymnosperms
 - ◆ abiotic and environmental conditions and challenges not comparable to the recent ones

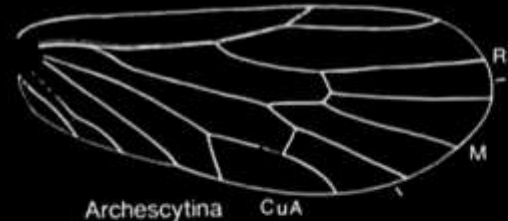
Paleorrhyncha

Permian 'Archescytinidae'

- miniaturisation
- homonomic venation of forewings and hind wings
- differentiated placement of rostrum base
- antennae 10-segmented with rhinaria
- elongated ovipositors
- nymphs cryptic, flattened
- gall-making
- trophic relationships with seed ferns and early gymnosperms



Permoscytina



Paleoscytina

Uraloscytina



Sarbaloscytina



Sojanoscytina



Permopsylla



Kaltanoscytina

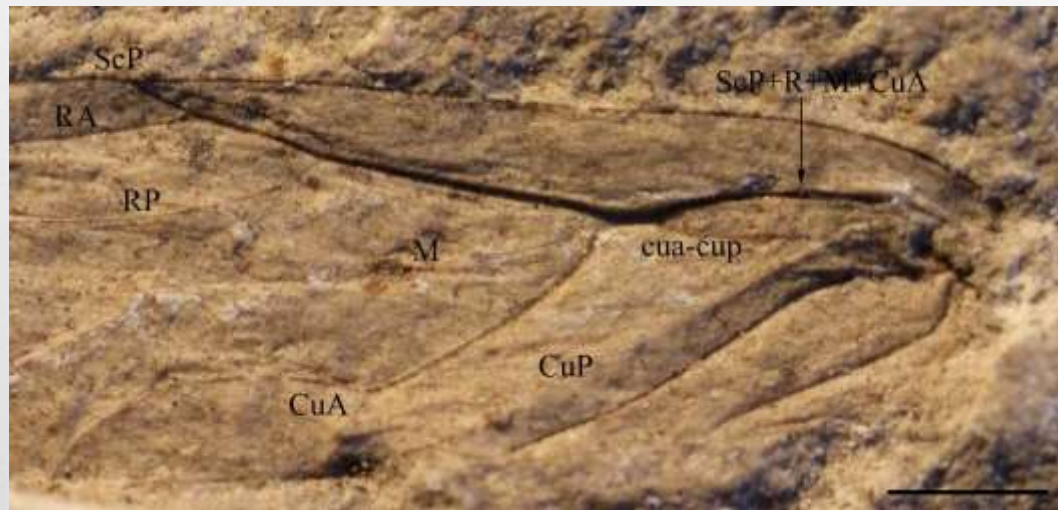


Eoscytina

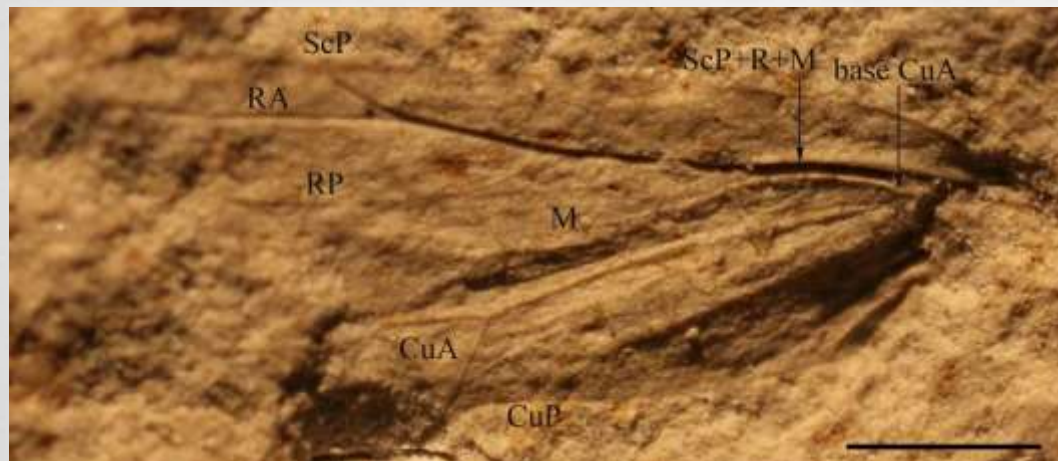
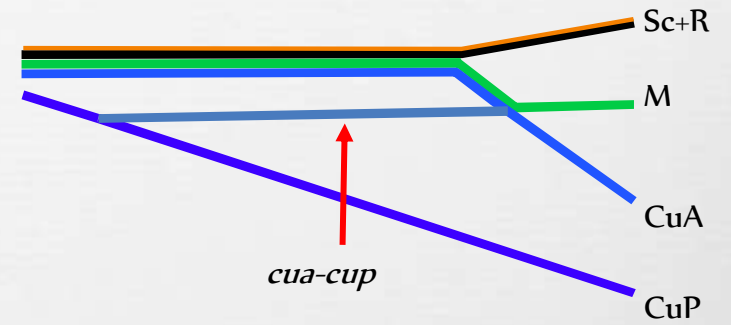


Bekkerscytina

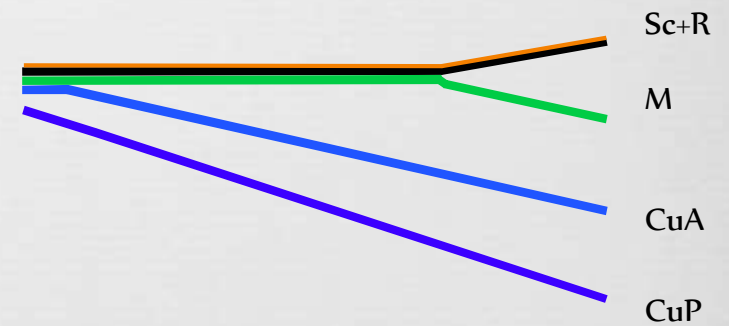
Hemiptera: Paleorrhyncha



Archescytina permiana



Lithoscytina cubitalis



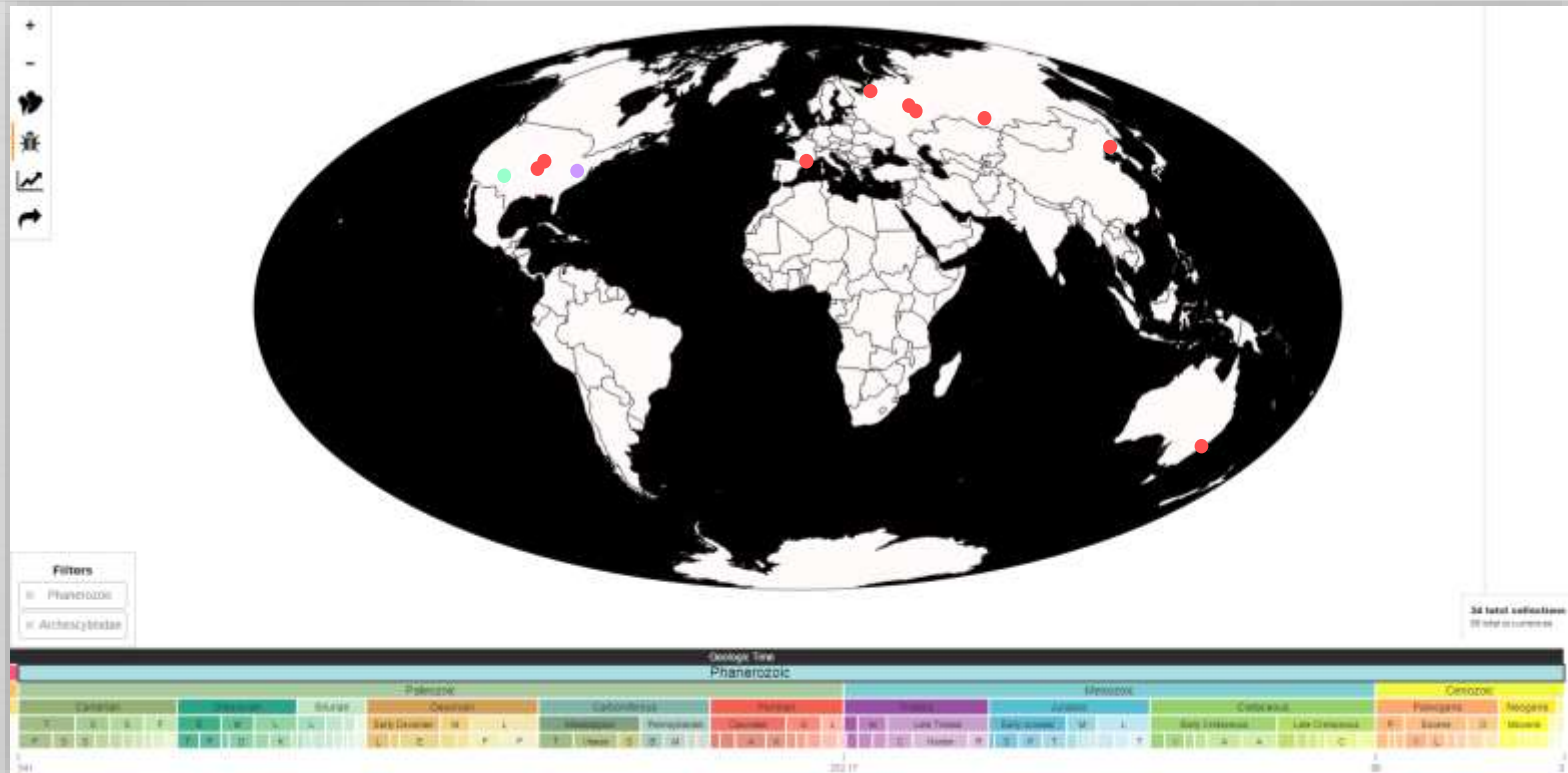
HOMOPTERA: Archescytinidae: *Permopsylla americana* Tillyard, 1926

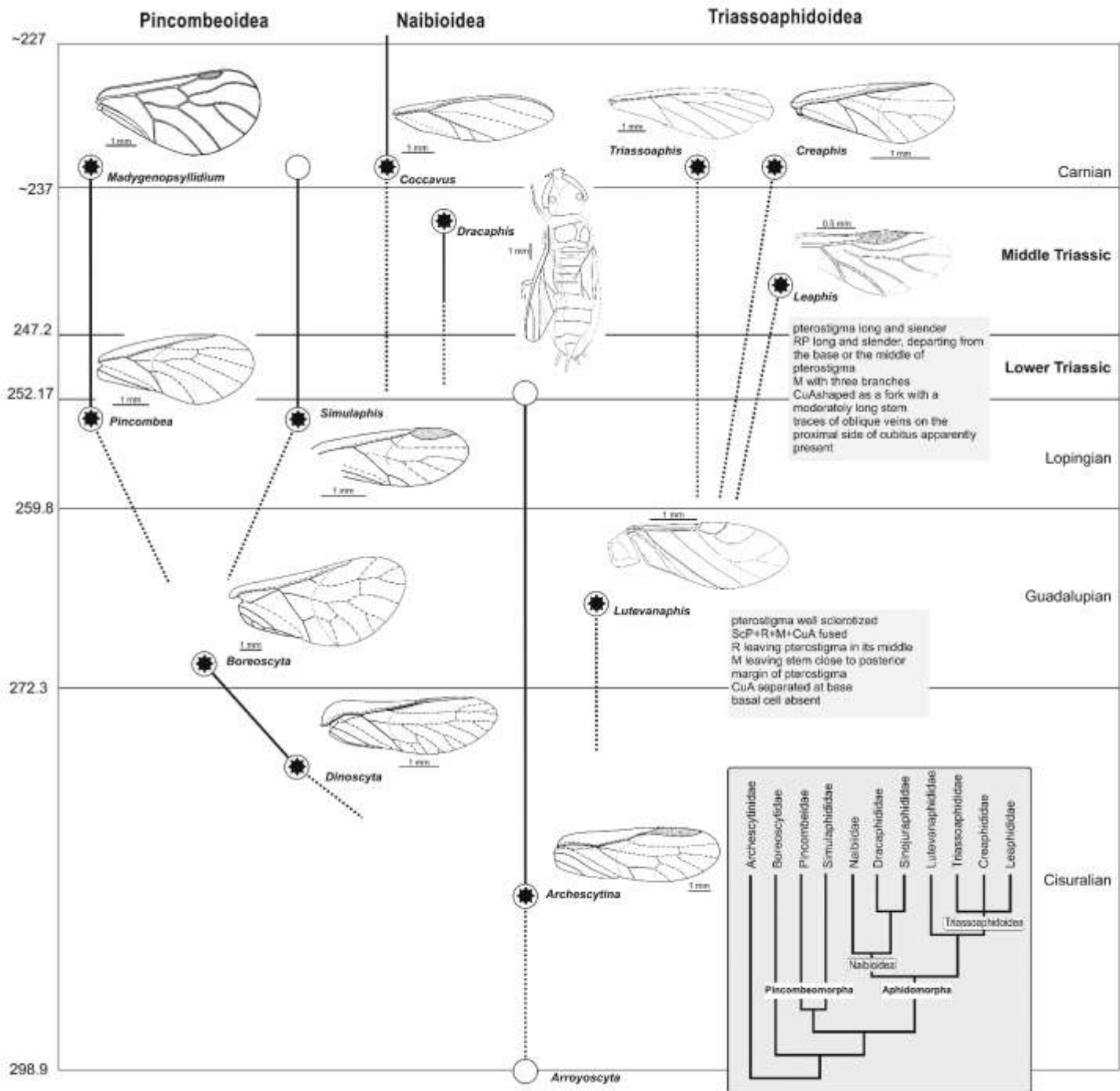
Paleorrhyncha

Fam: Archescytinidae

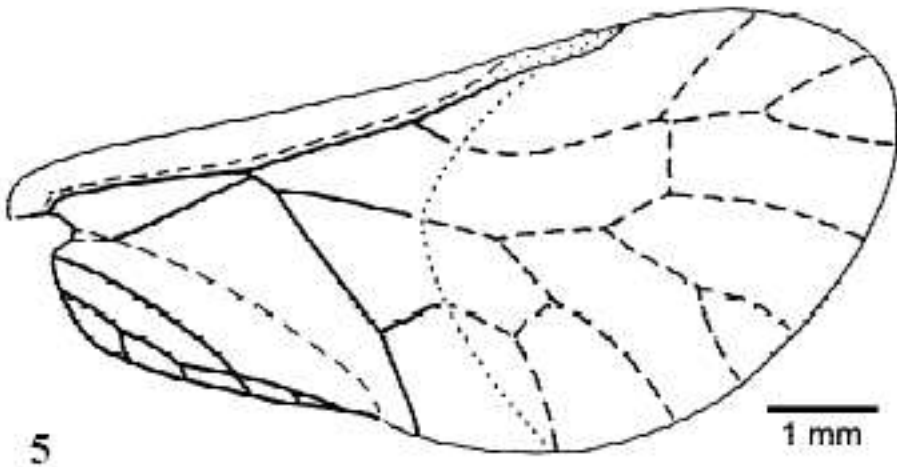
- = Permopsylliidae
- = Lithoscytinidae
- = Maueriidae
- = Permoscytinopsidae
- = Uraloscytinidae
- = Maripsocidae
- = Kaltanaphididae

R9-2002-003a, Raasch Sta. 9, Nobel County, Oklahoma. 0.05 mm/div.
Cicld 12/02 by Joseph Hall. Id by Roy Beckemeyer, May, 2003.



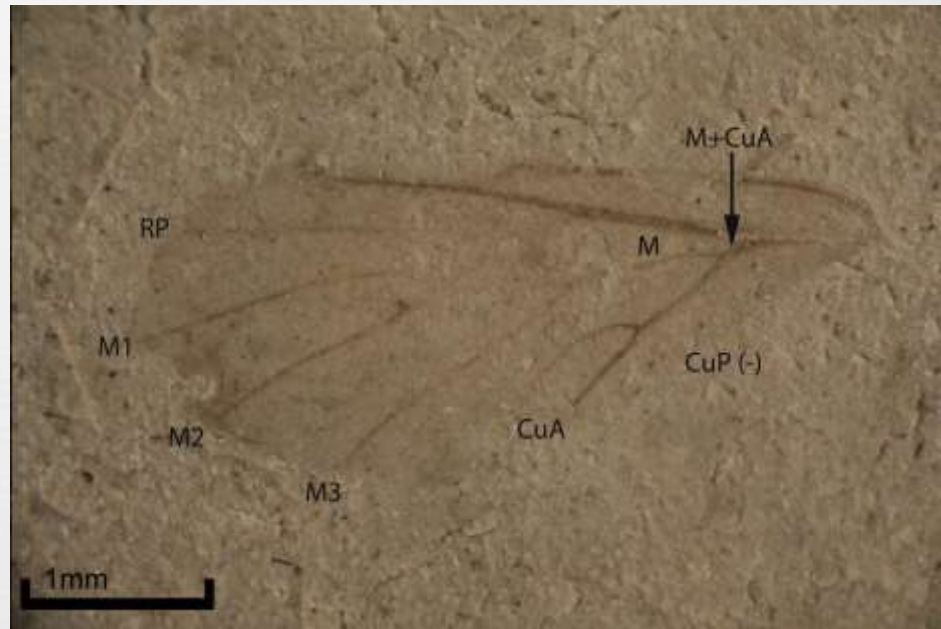


Hemiptera: Sternorrhyncha



Figs 4–5. *Boreoscyta nefasta* Becker-Migdisova, 1949. PIN 3353/716, Middle Permian of North European Russia; 4 — forewing; 5 — venation of forewing.

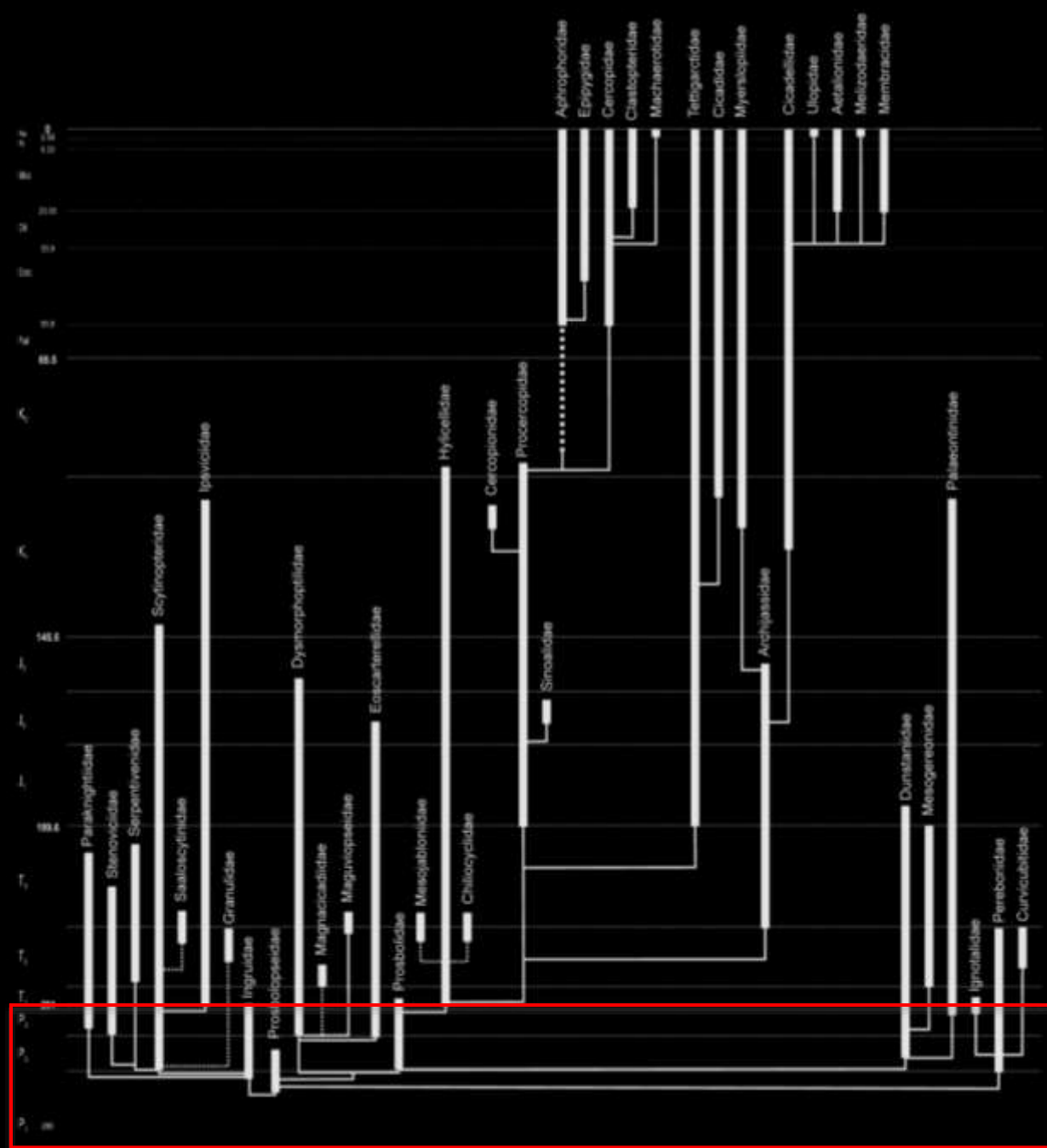
Boreoscytidae



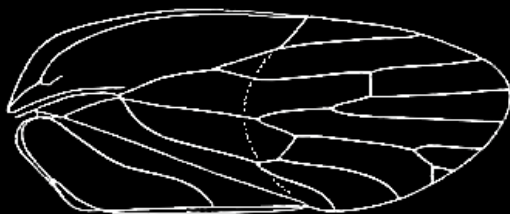
Pincombea parvifurcata
Pincombeidae

Cicadomorpha

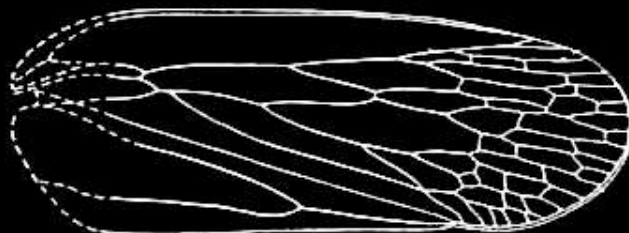
- long basicubital triangle preserved;
- basal cell elongated;
- costa enlarged with carina;
- ScP shifted from the stem R+M+CuA at base;
- tendency to fusion of M+CuA apicad of basal cell
- polymerisation of veins
- enlargement of size;
- shift to xylem-feeding;
- symbionts
- specialisation to sucking of cell content (miniaturisation);
- enlargement of frontoclypeus and salivary pump;
- spines and setae on legs;
- jumping legs;
- free-living nymphs;
- sound apparatuses



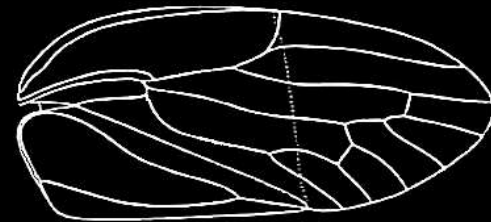
relationships of the Cicadomorpha



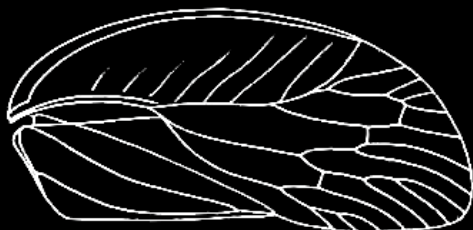
Permocicada integra
Prosbolidae



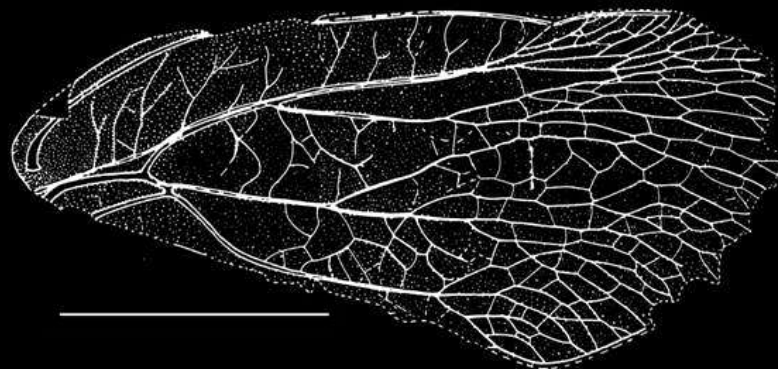
Scytophara extensa
Pereboriidae



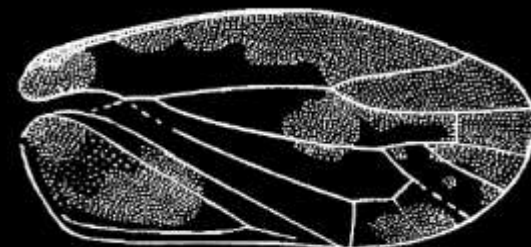
Scytoneurella major
Ingruidae



Prosbolopsis ovalis
Prosbolopseidae:
Prosbolopseinae



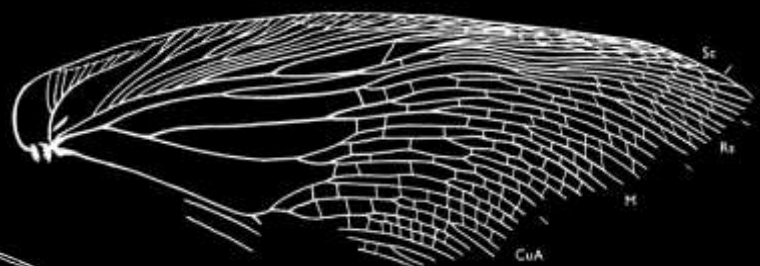
Gondwanaptera capsii
Pereboriidae



Scytinoptera kaltanica
Scytinopteridae



Prosboloneura kondomiensis
Prosbolopseidae: Ivaiinae



Ignotala mirifica
Ignotalidae

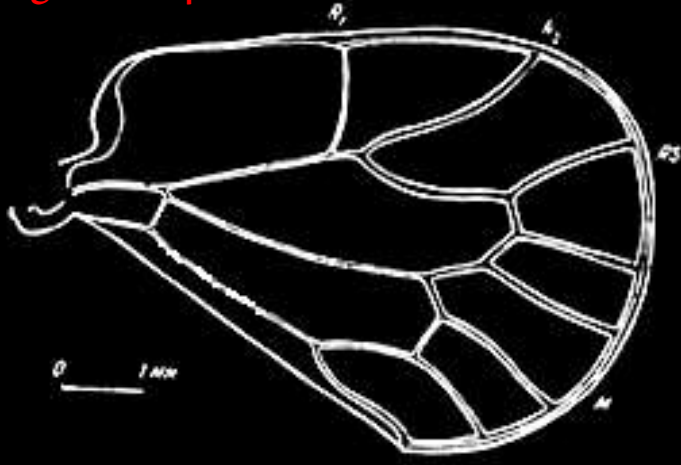


Stenoglyphis kimbiensis
Palaeontinidae



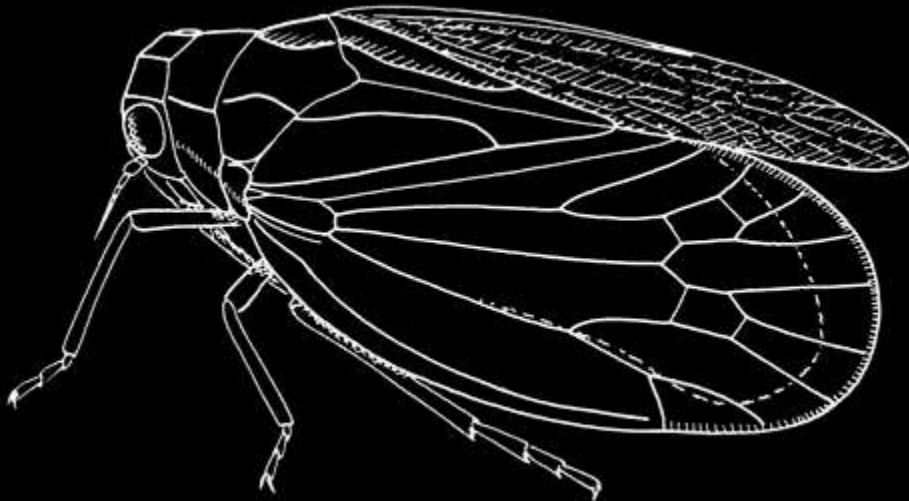
Paraknightia magnifica
Paraknightiidae

Fulgoromorpha



Coleoscyta sp.
Late Permian

Coleoscytidae were highly specialised
with distinct microbrachypterism of tegmina



Surijokocixius tomiensis
Surijokocixioidea: Surijokocixiidae
Late Permian

early Fulgoromorpha

short basicubital triangle of tegmen

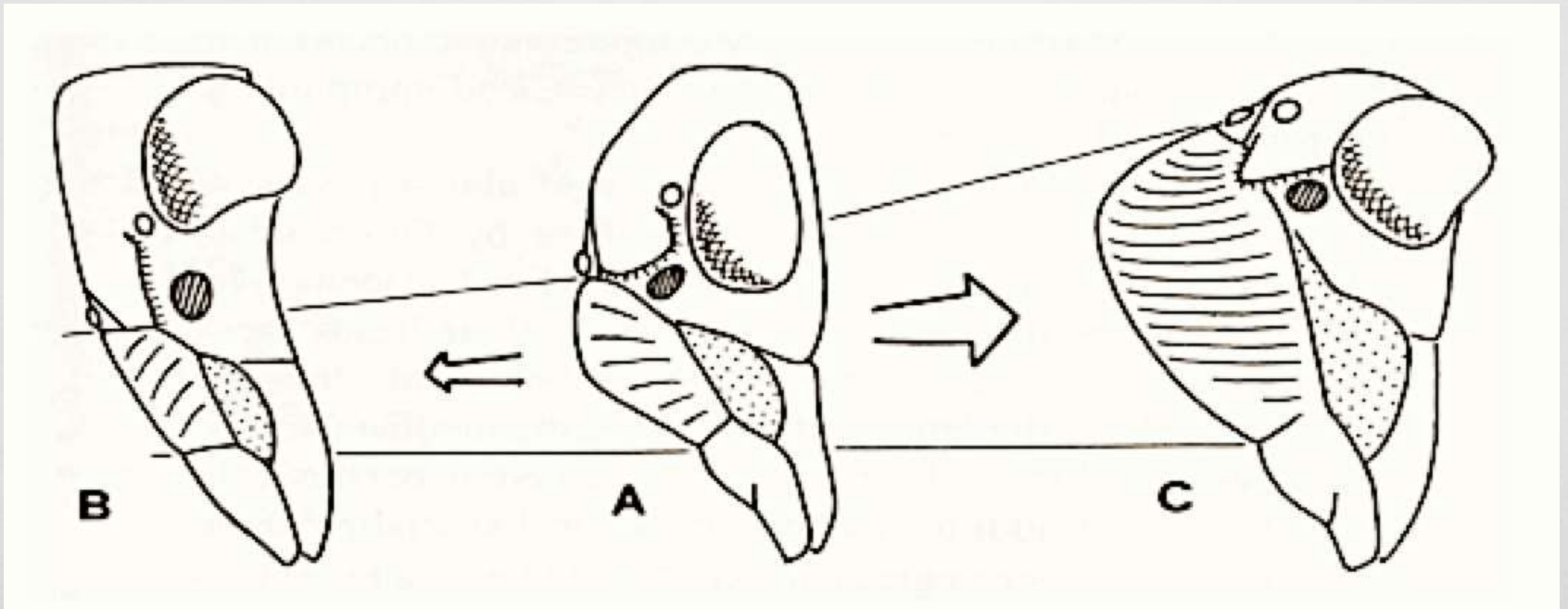
longitudinal carinae on pronotum and mesonotum

head capsule strengthened with carinae

bases of antennae below the compound eyes

? modifications of head capsule structure

? median ocellus present, shifted down to frontoclypeal suture



Episode 2



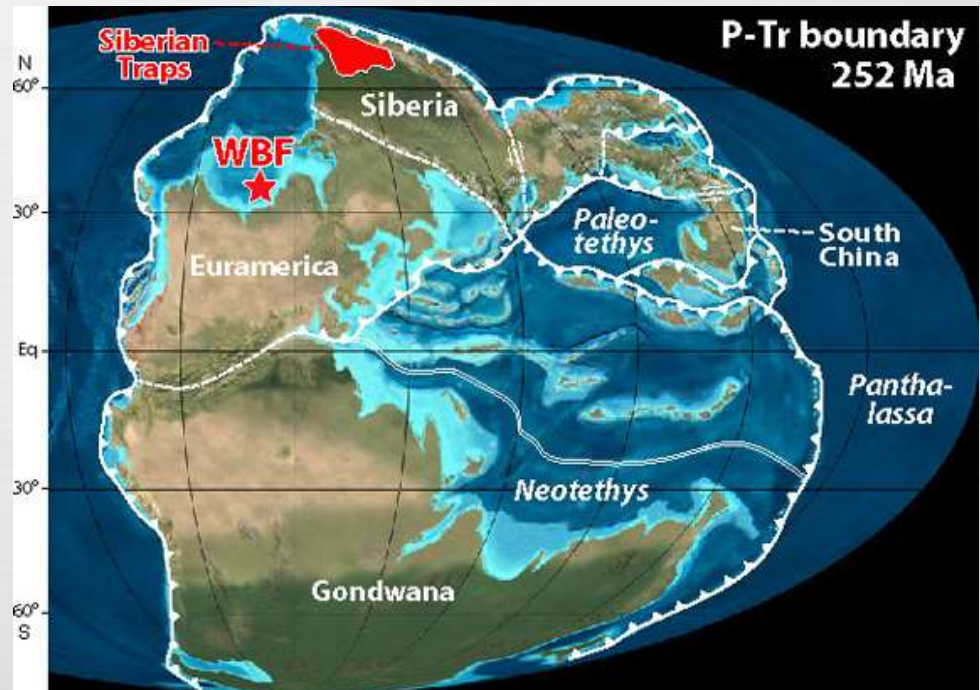
GREAT PERMIAN-TRIASSIC
EXTINCTION AND REBUILDING THE
DIVERSITY

Permian-Triassic mass extinction

- 252.28 Ma ago;
- the Earth's most severe extinction event (up to 96% of all marine species and 70% of terrestrial vertebrate species);
- the only known mass extinction of insects.



*“Daddy’s going to make some
extinctions, darling”*



Fossils from earliest Triassic, just after extinction, are virtually unknown

- ◆ Archesctynidae seems to gone extinct
- ◆ First records of the Hemiptera from the Middle Triassic times:
- ◆ Various Sternorrhyncha – Aphidomorpha, Pincombeomorpha, Naibioidea and probably earliest Coccoomorpha; Protosyllidiidae
- ◆ Fulgoromorpha not diverse – latest Coleoscytidae and Surijokocixiidae
- ◆ Cicadomorpha highly diversified – shift from phloem-feeding to xylem feeding in the Clypeata lineage
- ◆ Scytinopteroidea highly diversified and specialized
- ◆ diversification of Coleorrhyncha: Progonocimicidae
- ◆ earliest true bugs – Heteroptera: Nepomorpha and Dipsocoromorpha

which was the reason of shift to xylem feeding in the Clypeata?

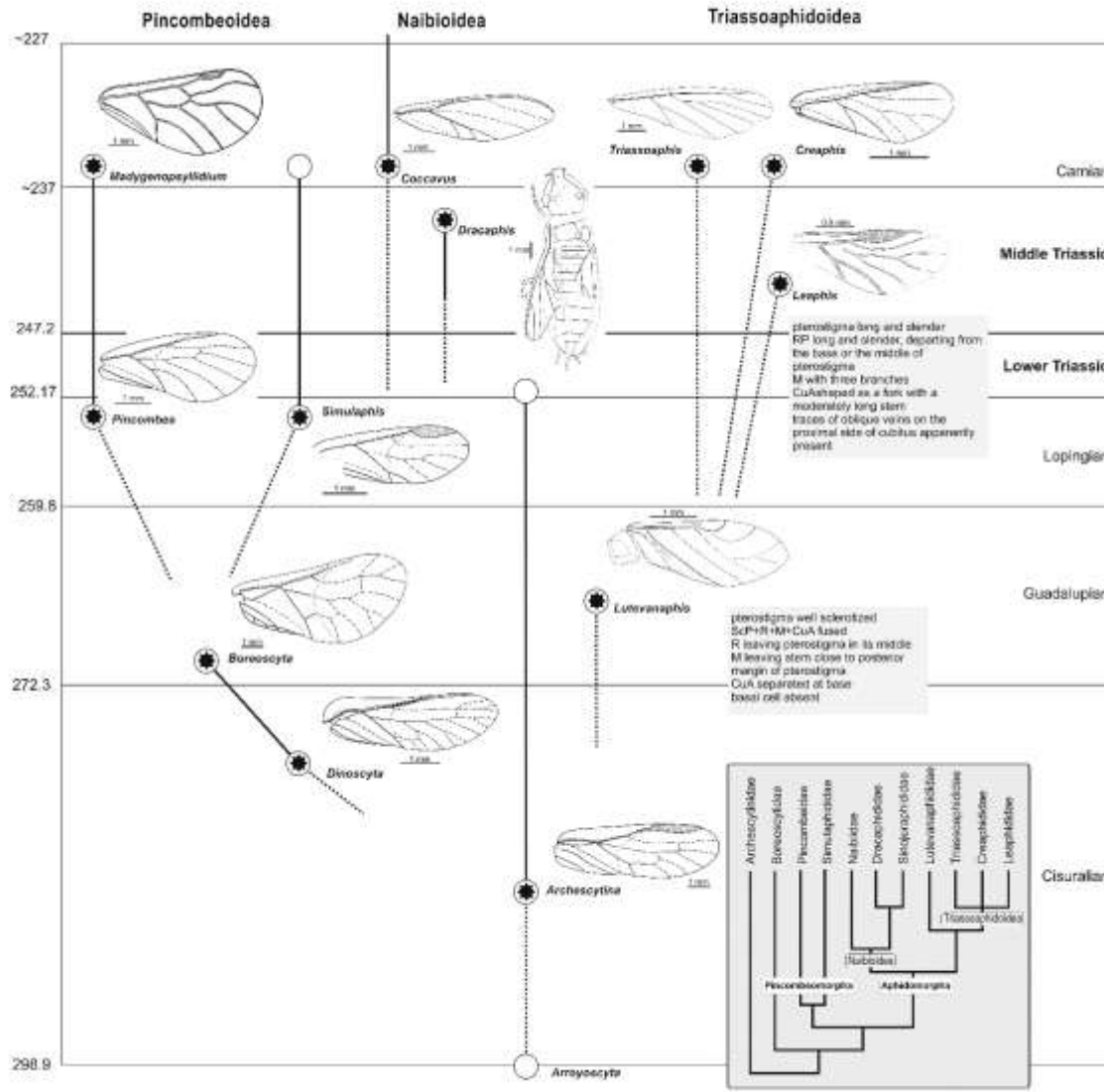
earliest endosymbiotic relationships retained in the modern Cicadomorpha: Clypeata?

shift to cryptic, endogeic life-style in earliest Coccoomorpha?

scavenging and predatory behaviours in the earliest Heteroptera

sound production with wings – Cicadomorpha: Dysmorphoptilidae

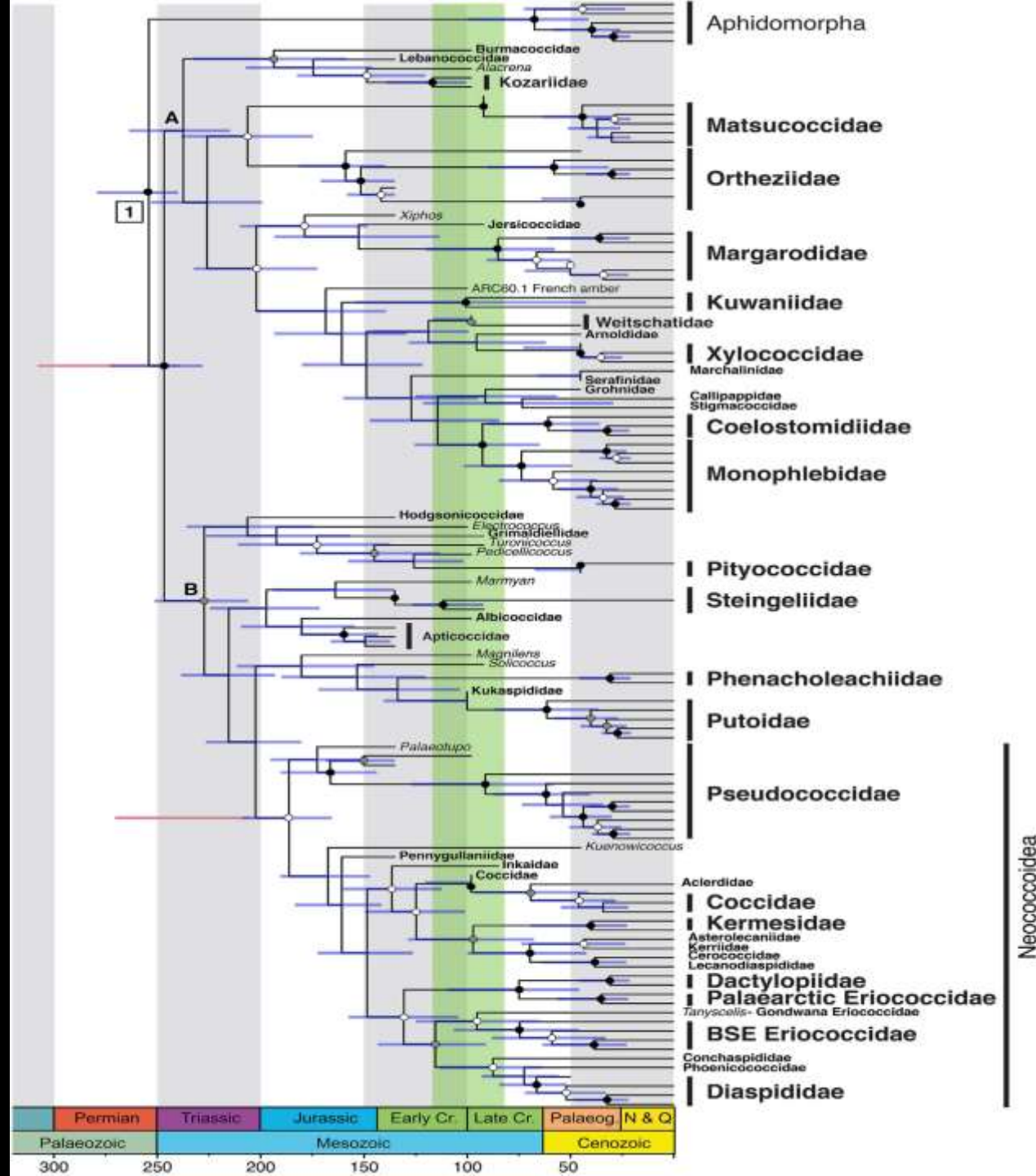
Sternorrhyncha: Aphidomorpha

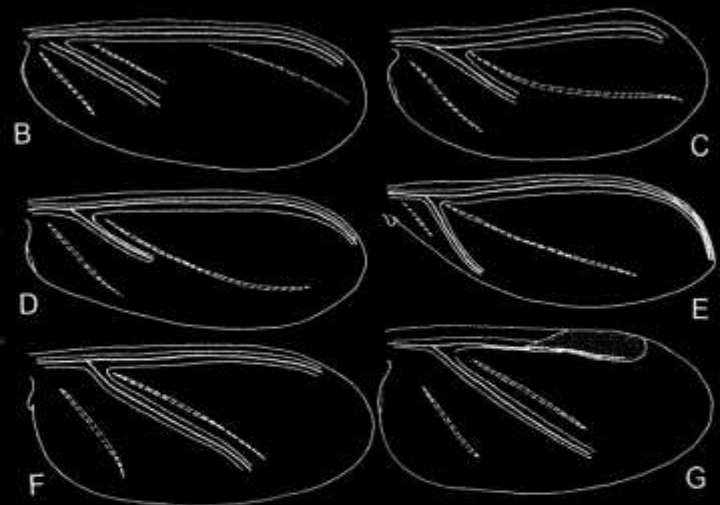
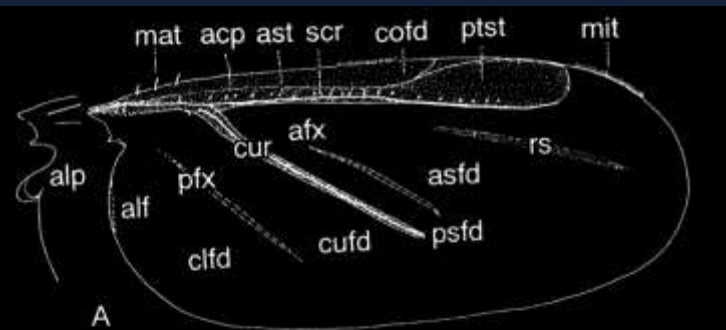


- first diversification during the Triassic
- modifications of the wing shapes from oval to triangular
- reduction of basal cell
- elongated common stem
 $ScP+R+(M)+CuA$
- reduction of venation
- loss of vein M connection with stem
- costalization
- reduction of anal lobe (clavus)
- dipterization (?) and miniaturization
- oligomerization of antennal segments (?); primary and secondary rhinaria
- diploidal parthenogenesis (?)

Sternorrhyncha: Coccidomorpha

- first radiation in the Triassic (?)
- related to gymnosperms (mycorrhizal fungi?)
- transfer to live in litter, soil, on roots (?)
- lost of tarsal claw, legs transformed into digging organs (?)
- antennae with complete number of segments; without rhinaria, primitive sensorial organs, numerous sensilla trichoidea;
- motion and orientation (?)
- sexual dimorphism
- differentiation of chromosomal system
- fossil materials known since Jurassic/Cretaceous





Directions of Coccidomorpha evolution

males

- litter-living
 - dipterisation+polimophrizm
 - miniaturization → origin of pseudopupa
- fragility+feeding on above-ground parts of host-plants → composed chromosomal systems;
- feeding on plants → specialized digitulae;
- forewings placed aong the abdomen; venation reduced;
- reduction of hind wings to halteres;
- resting stadia (prepupa and pupa); sex determination

females

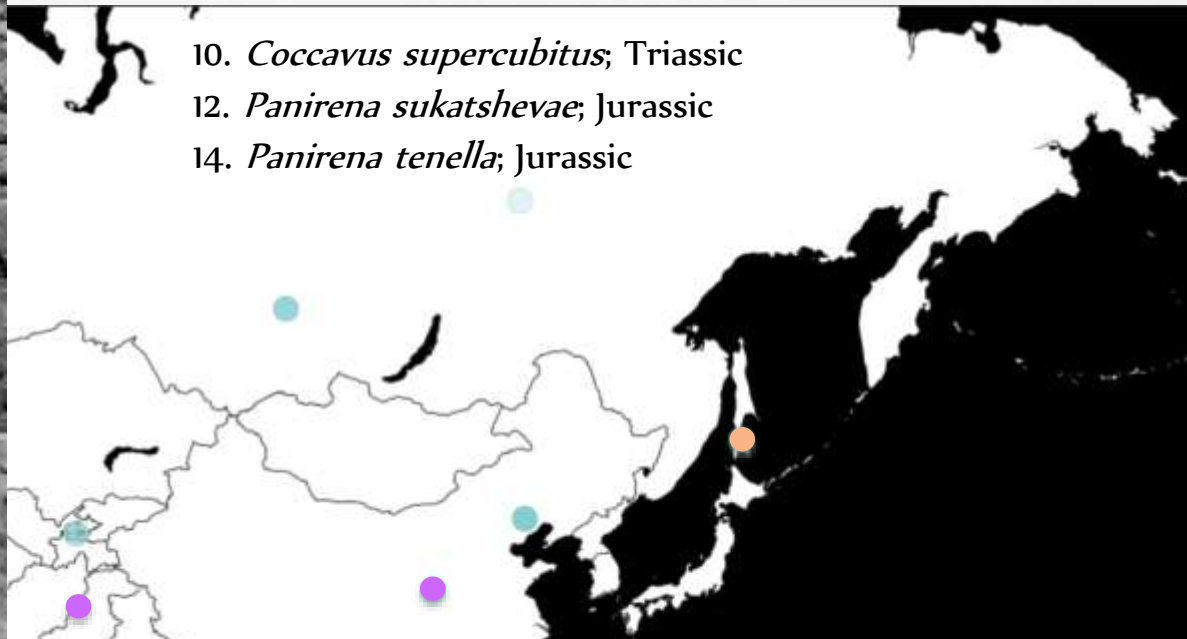
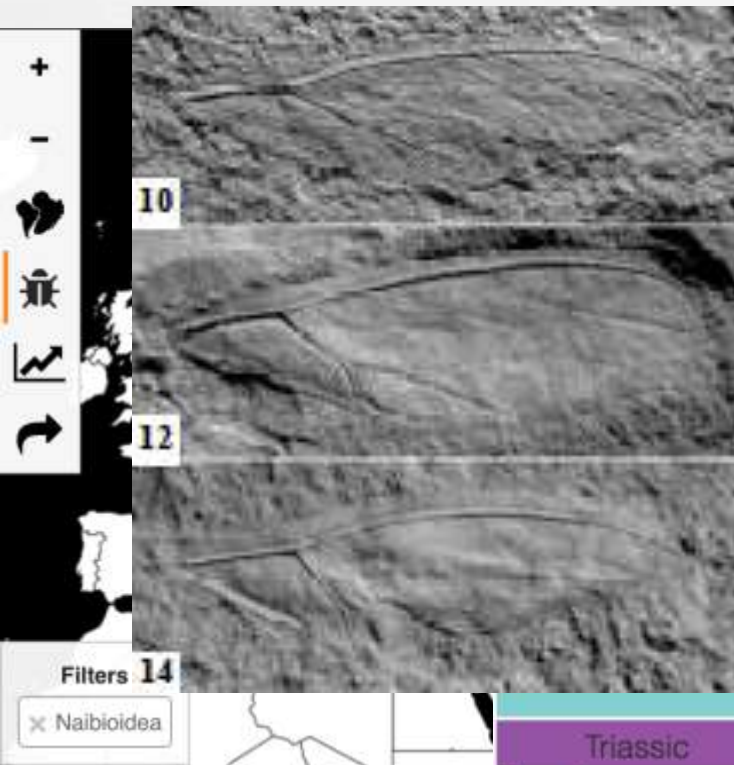
- litter-living
 - larvalisation (neoteny?), eggs in marsupium
- secondary, independent transfer in various lineages to feed on overground portions of plants → various systems of symbionts;
- morphological transformations due to sedentary habits; development of security systems

Outline, ridges and flexing patches of scale insect wing.

A – generalized (based on wing of *Weitschatus vysniauskasi* gen. et sp. n.), B–F – wings of species dealt with in the present paper. B – *Xylococcus grabenhorsti* sp. n., C – *Arnoldus capitatus* gen. et sp. n., D – *Arnoldus clavatus* gen. et sp. n., E – *Serafinus acutipterus* gen. et sp. n., F – *Grohnus eichmanni* gen. et sp. n., G – *Weitschatus stigmatus* gen. et sp. n. Wings enlarged to the same length independent of real size. Ridges shown as three parallel solid lines; flexing patches indicated by interrupted lines; pterostigma and sclerotized strips shown by dotting.

acp – alar cupolae, afx – anterior flexing patch, alf – alar fold, alp – alar lobe (pocket), asfd – anterior subcostal field, ast – alar setae, clfd – claval (anal) field, cofd – costal field or thickening, cufd – cubital field, cur – cubital ridge, mat – macrotrichia, mit – microtrichia, pfx – posterior flexing patch, psfd – posterior subcostal field, ptst – pterostigma, rs – „radial sector”, scr – subcostal ridge.

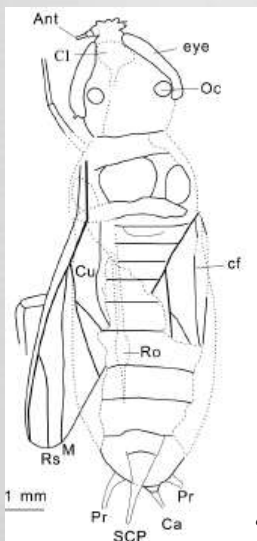
Naibioidea, Naibiidae, Sinojuraphidiaie and Dracaphididae – missing link or high specialization?



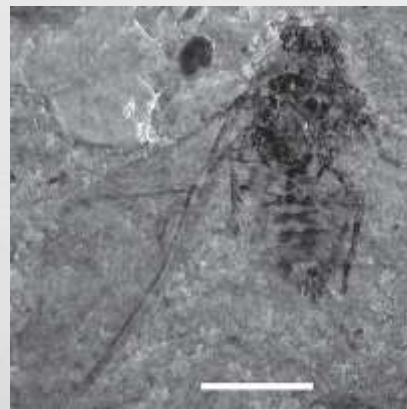
| Mesozoic | | | | | | | | | | | Cenozoic | | | |
|----------|---------------|--------|----------|---|---|------------------|------------|---|--|---|-----------|--------|---|----|
| Triassic | | | Jurassic | | | | Cretaceous | | | | Paleogene | | | Ng |
| M | Late Triassic | | E | M | L | Early Cretaceous | | L | | | P | Eocene | O | M |
| | C | Norian | S | P | T | | A | A | | C | | Y | | |

Sinojuraphis ningchengensis

Naibia zherikhini; Eocene



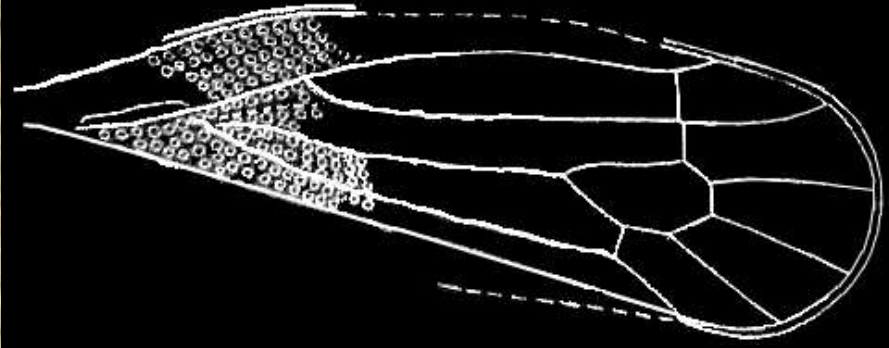
Dracaphis angustata



variety of Triassic Cicadomorpha



Dysmorphoptilidae



Hylicellidae



Dunstaniidae



Palaeontinidae

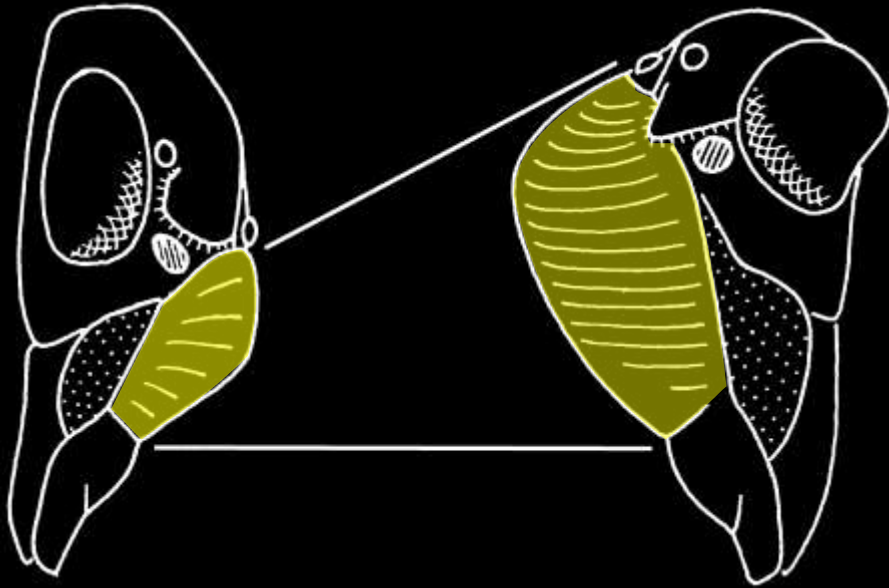
During the Triassic various lineages of the Cicadomorpha were present

Episode 3



XYLEM-FEEDING

Clypeata



- enlarged, swollen frontoclypeus, with distinct salivary muscle traces;
- frons with median ocellus shifted dorsally;
- xylem-feeding;
- nymphs (primarily) living underground;
- the first group with distinct adaptations for jumping;
- protection of body by the liquid produced by Malpighian tubules – brochosomes in Membracoidea
- development of spines and setae of legs in relation to covering the body with liquid and brochosomes;
- endosymbiotic *Sulcia* and other bacteria

Why ancestors of Clypeata shifted their food-source?

New gymnosperm plants available as food source?

Development of defensive mechanisms in gymnosperm plants?

Change in food-plants physiology?

Competition with Sternorrhyncha?

Cicadomorpha: Clypeata

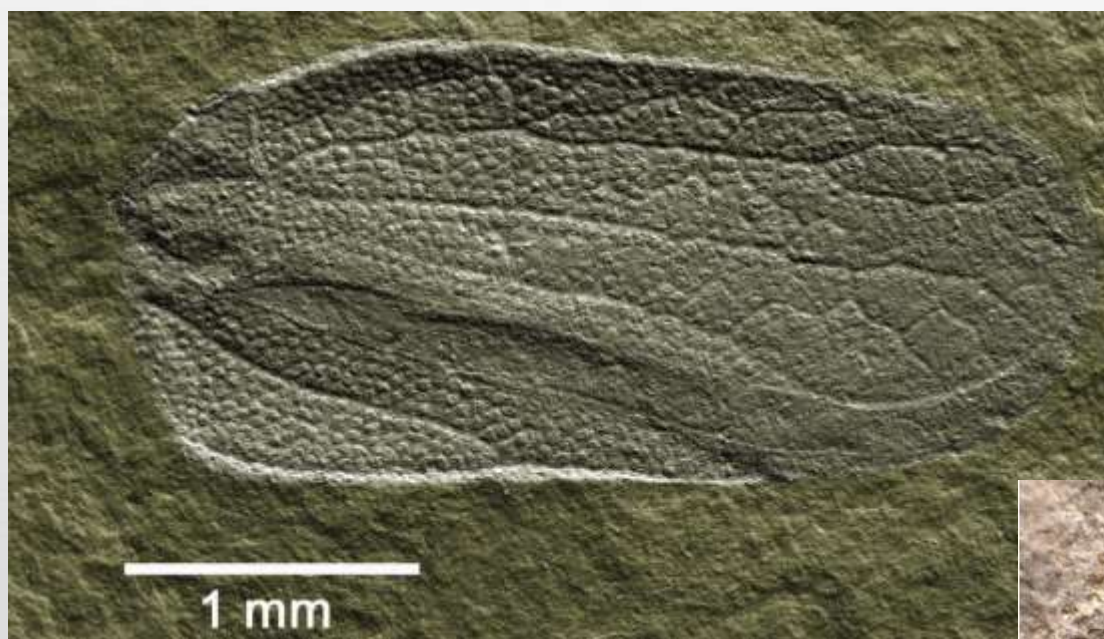
- ❖ The only surviving group of Cicadomorpha, present in the Recent fauna
- ❖ The recent groups are descendants of the Hylicelloidea
- ❖ Earliest Archijassidae in Australia



Mesojassus ipsviciensis
Triassojassus proavitus



Heseneuma hammelburgensis Brauckmann et Schlüter, 1993 – taxonomic position uncertain



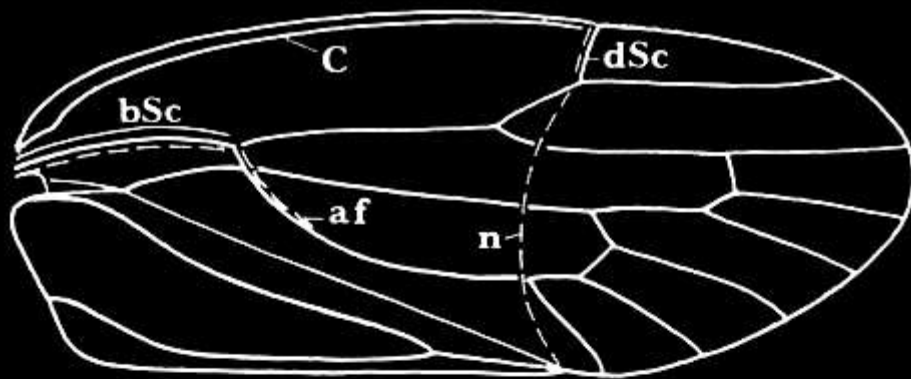
Ipsvicia langenbergensis Barth *et al.*, 2011

Ipsviciidae: Scytinopteromorpha

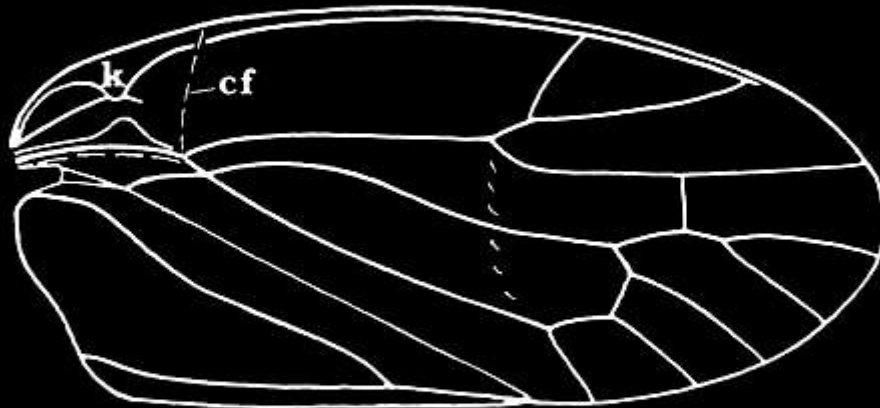
Episode 4



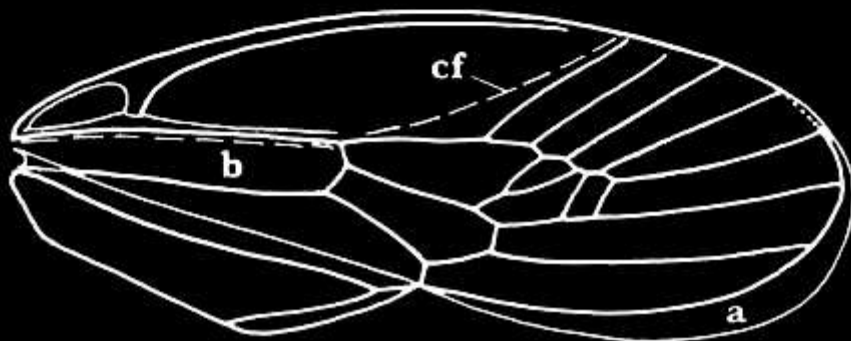
PREDATION



Prosbolopseidae (Cicadomorpha)



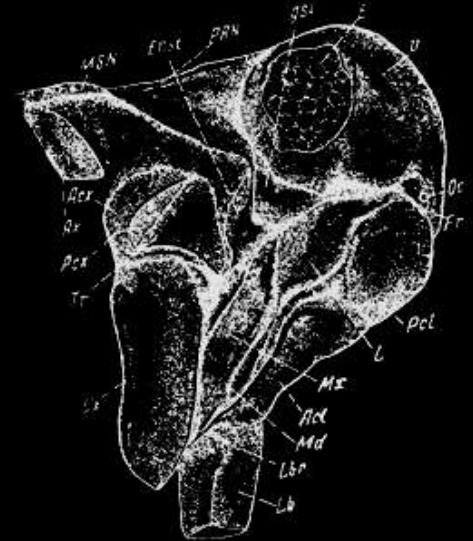
Scytinopteridae (Cicadomorpha s.l.)



Archegocimicidae (Leptopodomorpha)



Prosbolopseidae



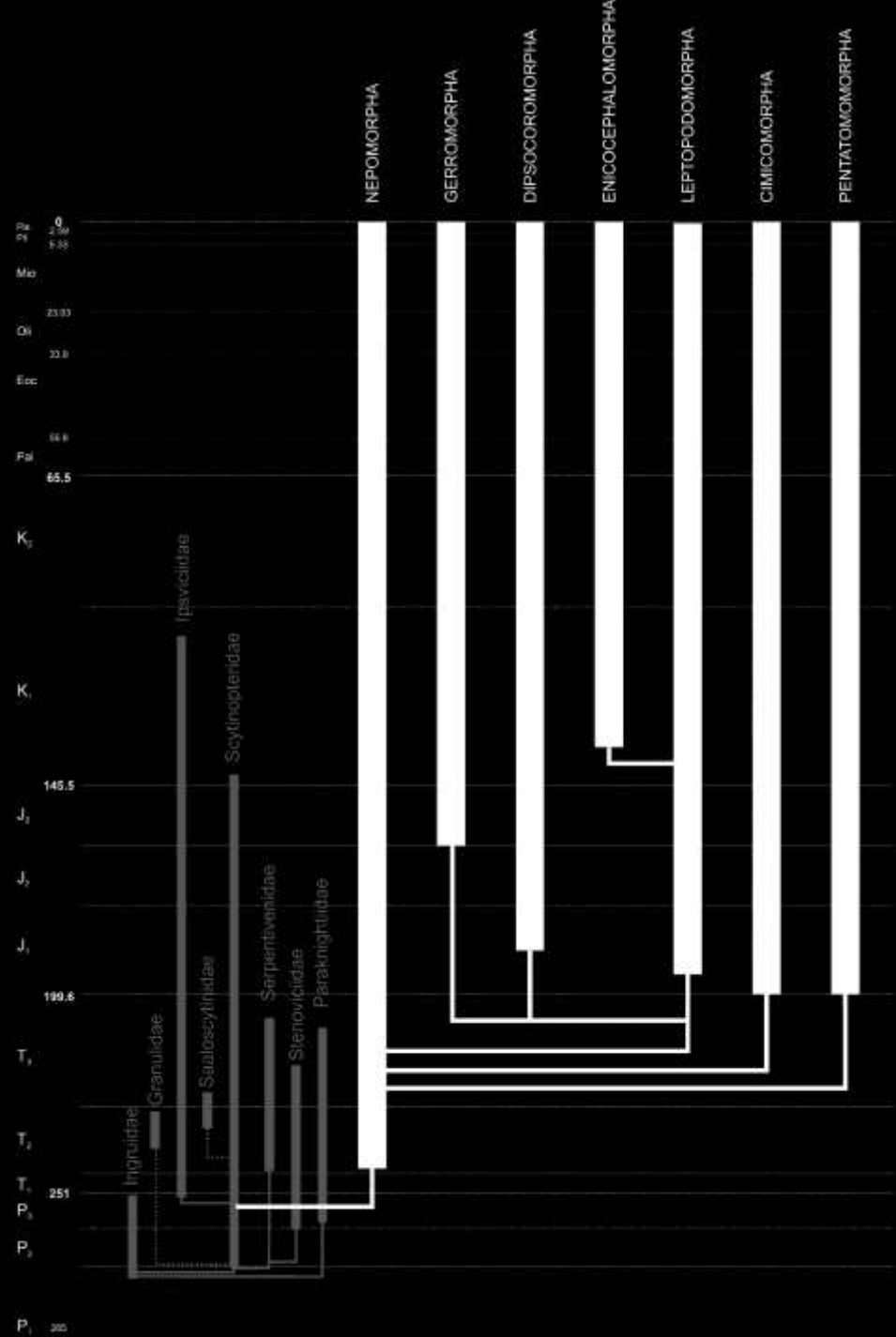
Scytinoptera sp.



Saldula sp.

Heteroptera

- fossil record since Middle Triassic;
- neotenic Scytinopteridae (?);
- nymphal features retained;
- body flattened;
- shift of feeding through saphrophagy (?), scavenging to carnivory;
- antennae 5 (4)-segmented;
- increased mobility of head;
- shift of rostrum to front of head; head opistognathous;
- additinal sclerite – gula;
- tegmina with costal fracture;
- Druckknopfsystem – clip holding tegmen at repose;
- shortened clavus, membranes of tegmina overlapped
- distinct elongation of basal cell;
- membrana tegminis softer;
- secondary herbivory / carnivory / blood-sucking



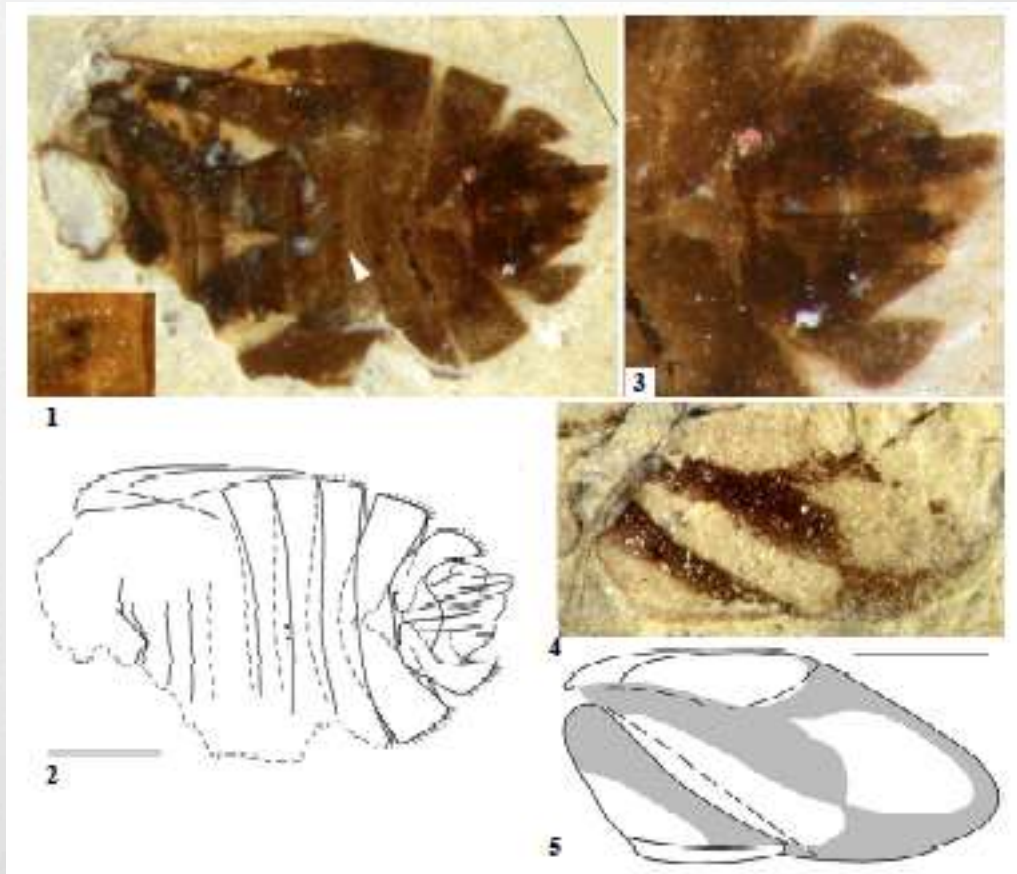
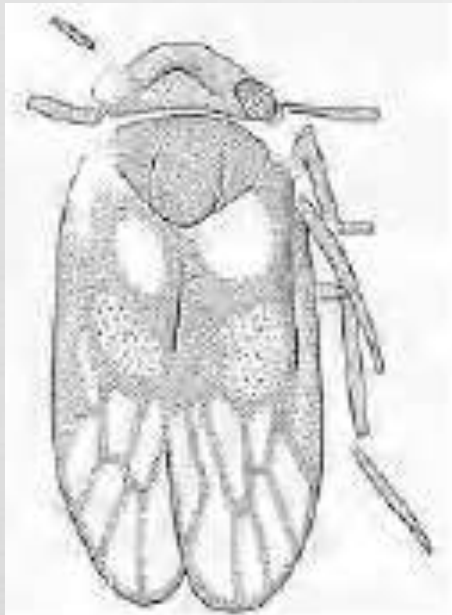
Appearance of the Heteroptera from scytinopteroids

- ◆ neoteny and structural simplification
- ◆ transition from 3D environment to 2D environments – shores and floating mats
- ◆ scavenging to predation
- ◆ development of costal fracture at apex of basal cell (substituting nodal flexion line), hypocostal pit mounting mesepimeral knob in repose (Druckknopfsystem)

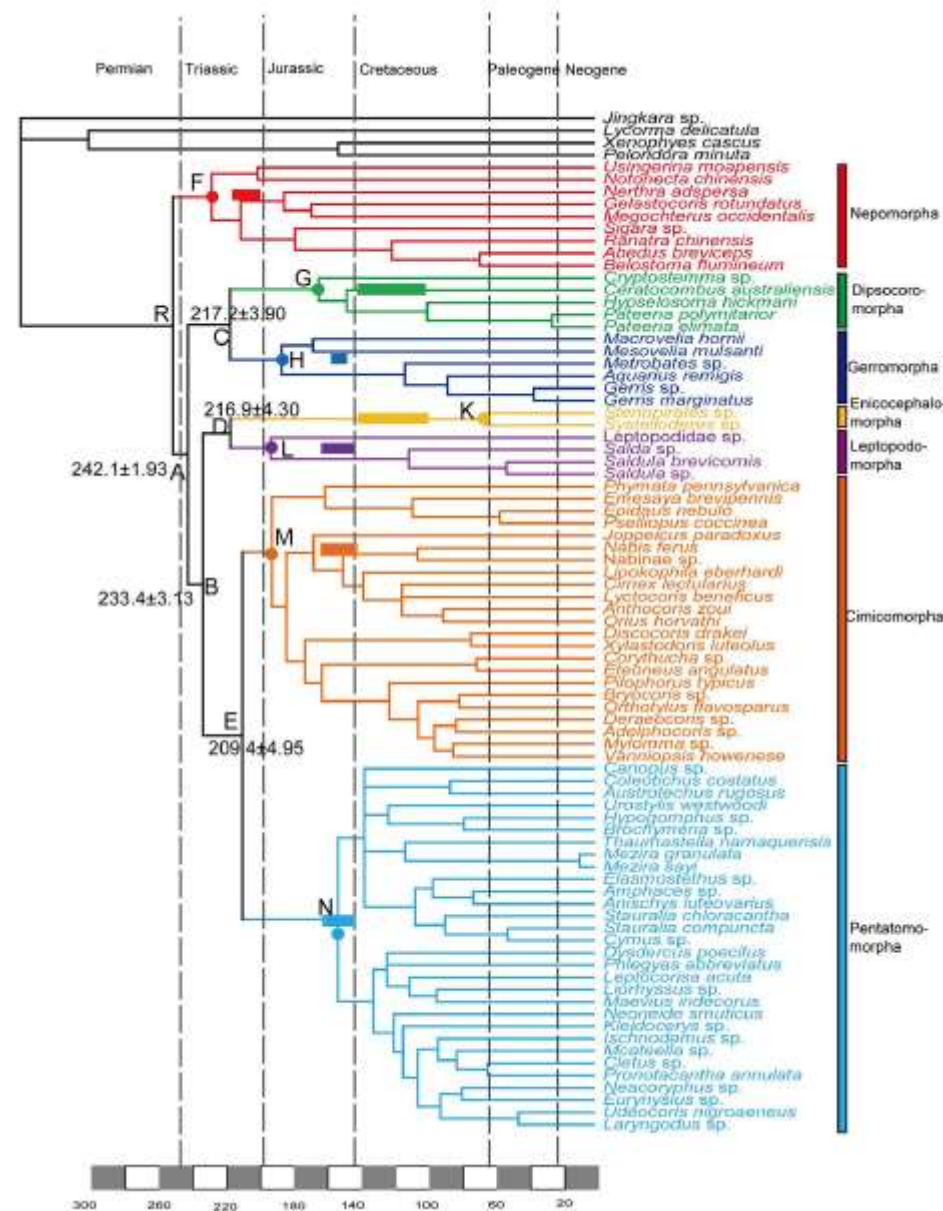
Arlecoris louisi Shcherbakov, 2012

Heteroptera: Nepomorpha: Naucoroidea: Triassocoridae

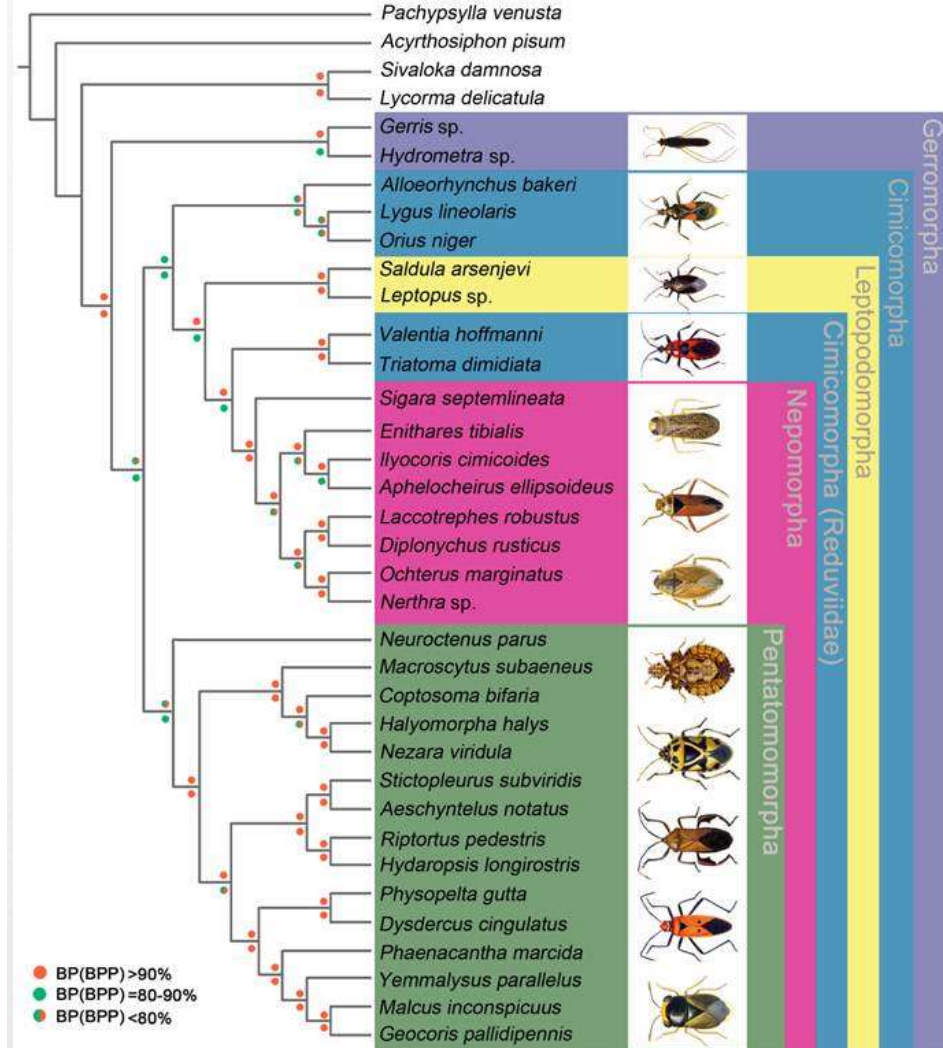
Heteroptera: Dipsocoromorpha?







Li M. *et al.* 2012
nuclear DNA

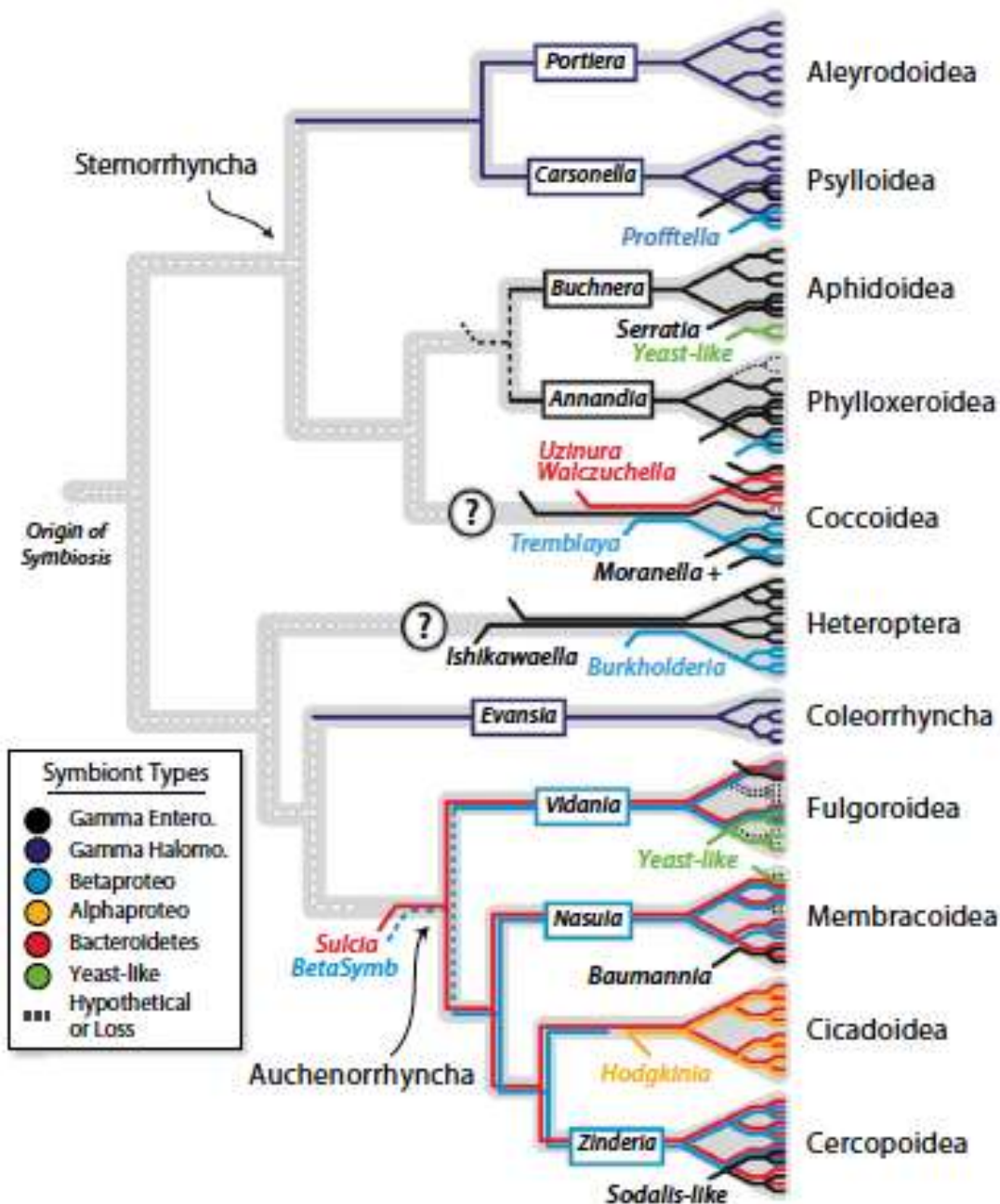


Li H. *et al.* 2012
mitochondrial DNA

Episode 5



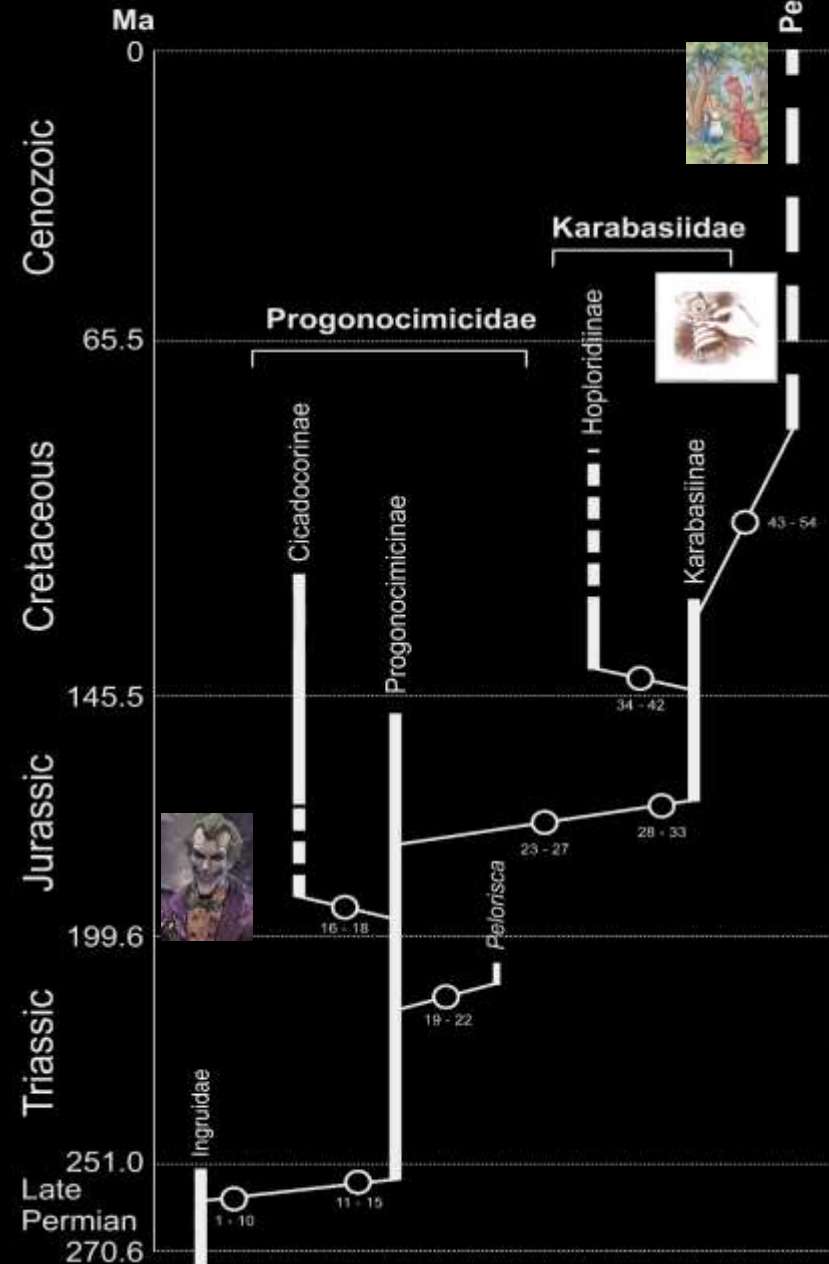
JURASSIC DIVERSIFICATION



Summary of the acquisitions and losses of heritable endosymbionts across sap-feeding insects in the order Hemiptera.

Coleorrhyncha

- originated in the Late Permian from Ingruidae (Scytinopteroidea);
- feeding on phloem of gymnosperms;
- flattened body;
- changes of head capsule structure (alveolarisation)
- supraantennal ledges fused over frontoclypeus;
- pronotum with paranota;
- asymmetry of tegmina due to overlapping of left over right – enlargement of membrane;
- membrane with appendix;
- wing-coupling apparatus of Heteroptera type;
- fore and mid tarsi 2-segmented;
- pygofer barrel-shaped, styli bent
- nymph flattened, cryptic, non jumping;
- imagines jumping;
- modern forms secondary in moss and litter
 - feeding on mosses (?) or fungi (?);

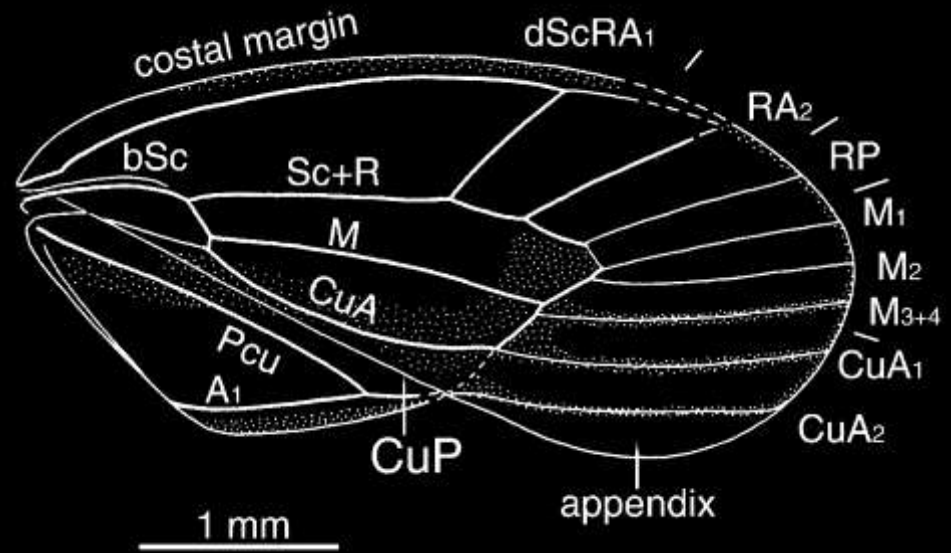




Mesocimex lini



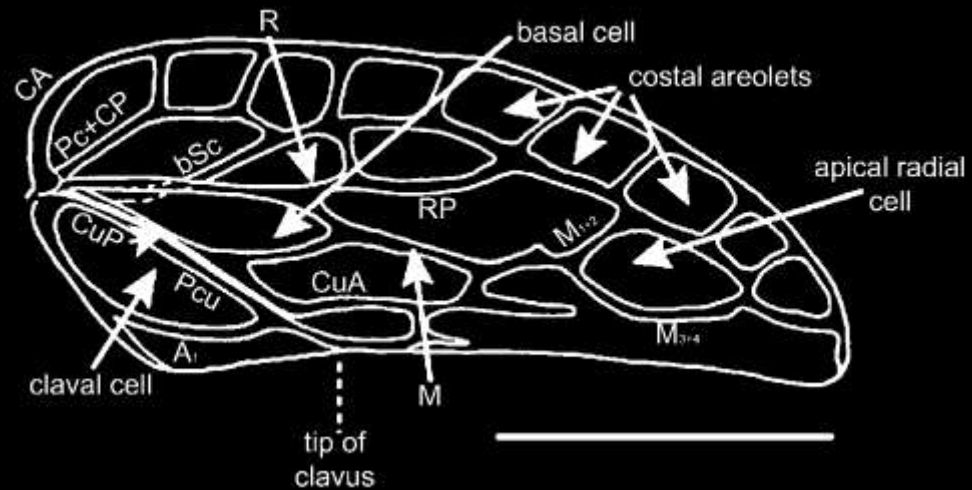
Karabasia plana



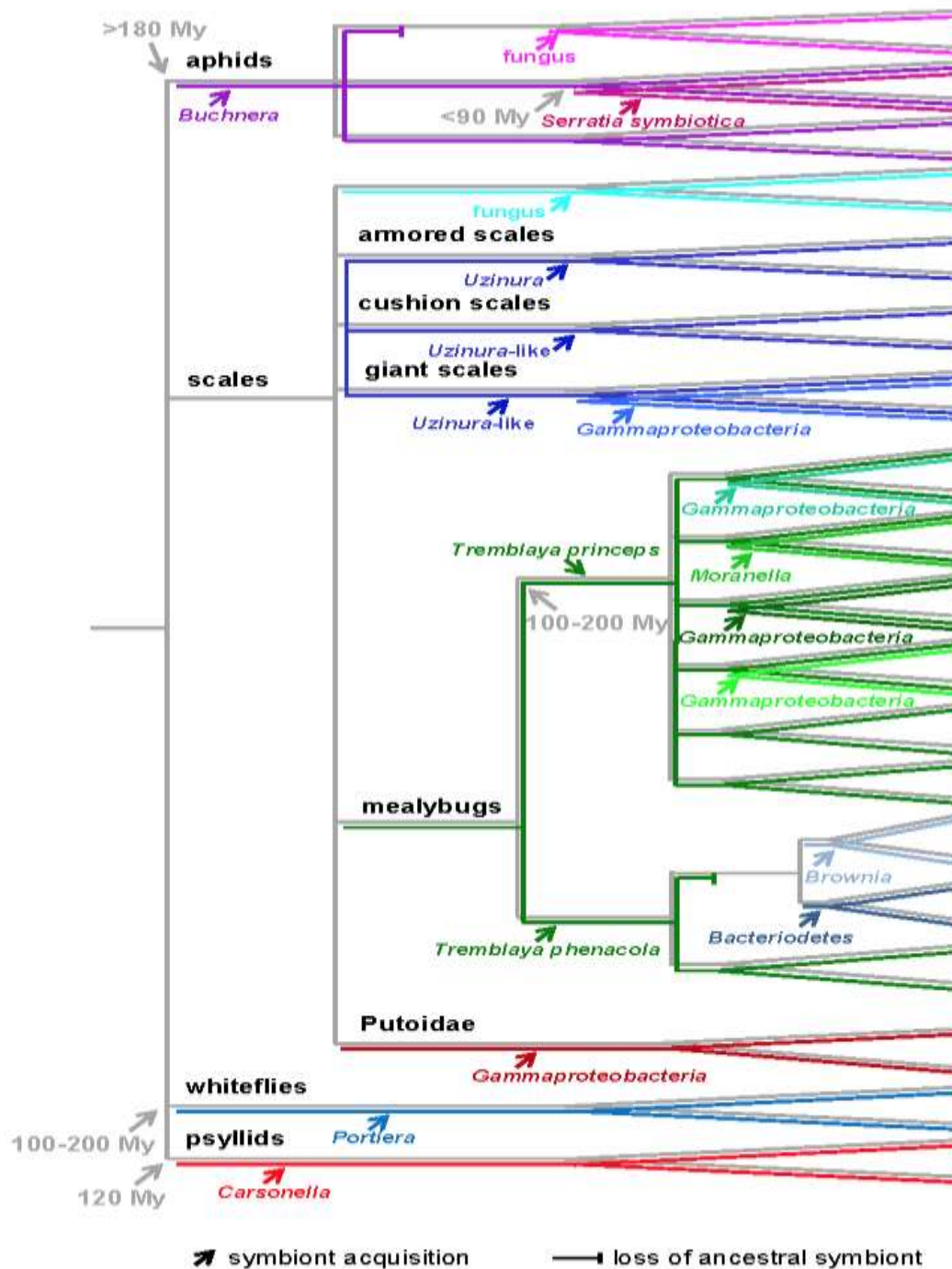
Eocercopsis similis



Hackeriella veitchi



Peloridium hammoniorum

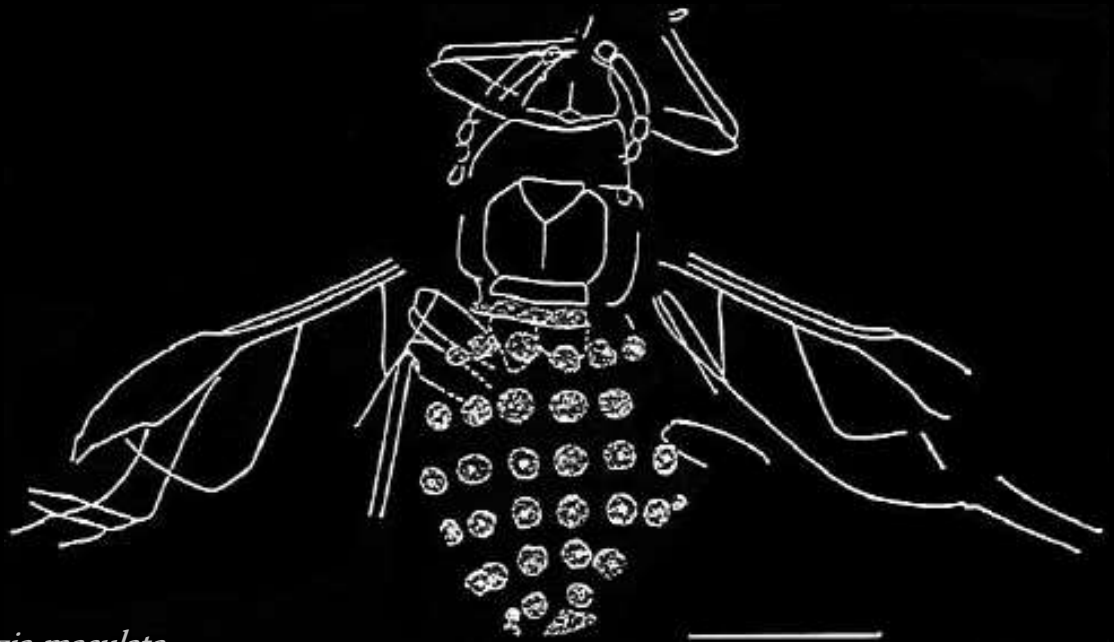


Multiple acquisitions and losses of symbionts among Sternorrhyncha

How strong is the influence of **Red King** on evolutionary traits among various sternorrhynchan groups?

Which are the advantages and perils of an evolutionary rabbit hole of heritable symbiosis?

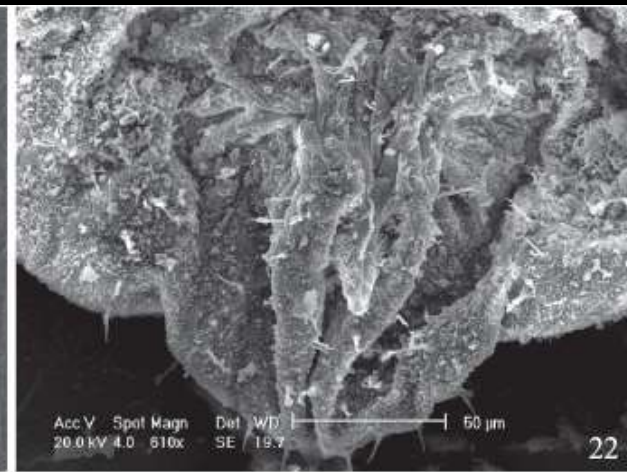
If and how strong this effect interferes with **Red Queen** and **Court Jester** activities?



Szelegiewiczia maculata
Szelegiewicziidae



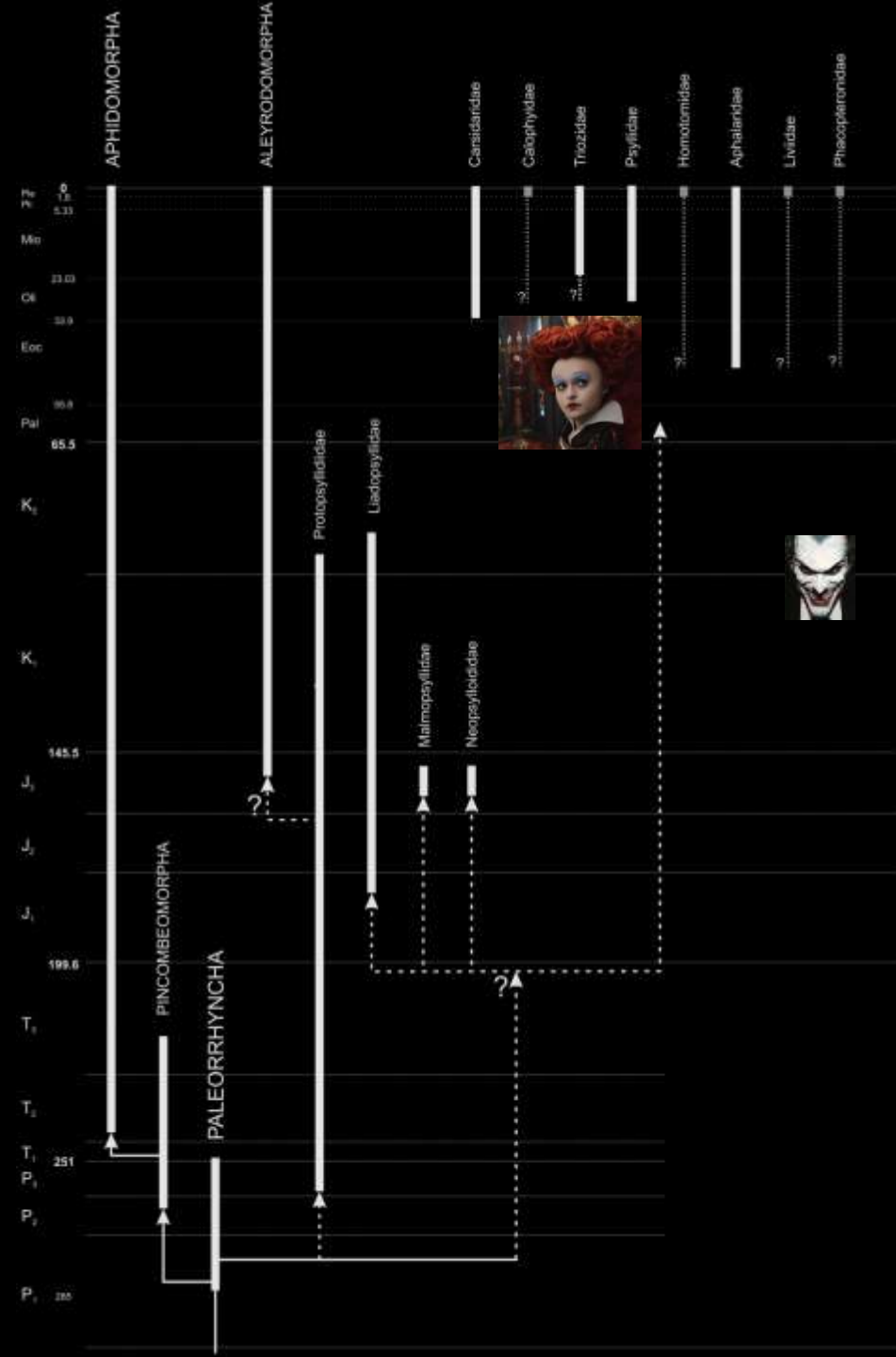
Aphis nerii (Aphididae) - cornicles



Pineus boernerii (Adelgidae) - ovipositor

Sternorrhyncha: Psyllaeformia

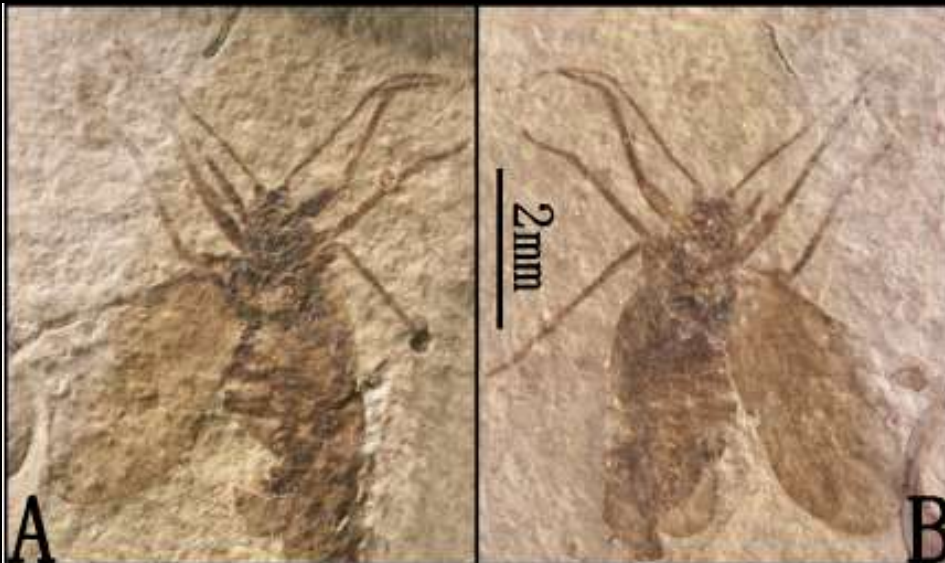
- separation in the Permian (?);
- retention of numerous features shared with Archescytinidae;
- diversification of Protopsyllidiidae in the Jurassic;
- origins of modern fauna related to Palaeogene radiation in concordance with angiosperms diversification;
- retained venational model;
- retained 10-segmented antennae;
- hind legs jumping;
- flattened nymphs;
- nymphs of Psylloidea with specialized setation;
- nymphs more strictly related to host-plants than imagines;



Carpenterella pusilla



Talaya batraba

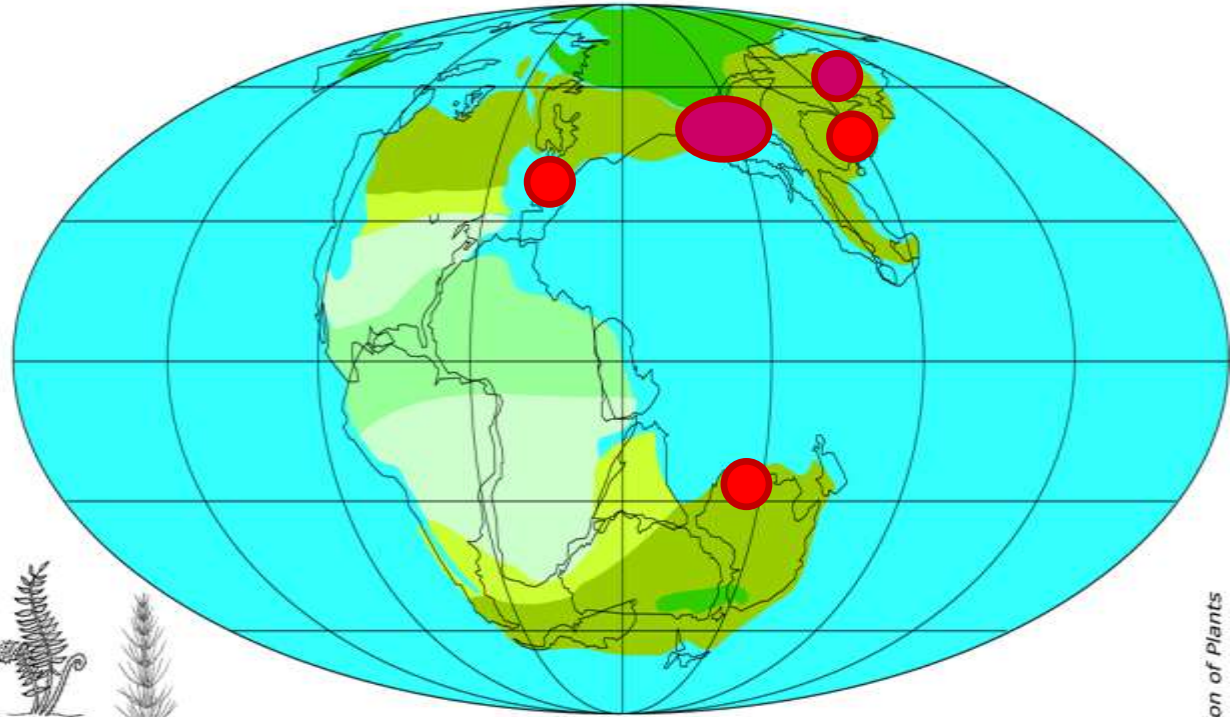


Poljanka hirsuta



Postopsyllidium emilyae

Early Jurassic (206-180 Ma)



Tropical
summerwet



Cycadales and Bennetitaes
(microphyllous)



Conifers
(microphyllous)



Ferns Sphenopsids

Subtropical
desert



Warm
temperate



Ferns



Sphenopsids



Cycadales and Bennetitaes
(macrophyllous)



Conifers
(macrophyllous)



Ginkgoales

Winterwet



Cycadales and Bennetitaes
(microphyllous)



Conifers
(microphyllous)



Ferns



Sphenopsids

Cool
temperate



Ginkgoales



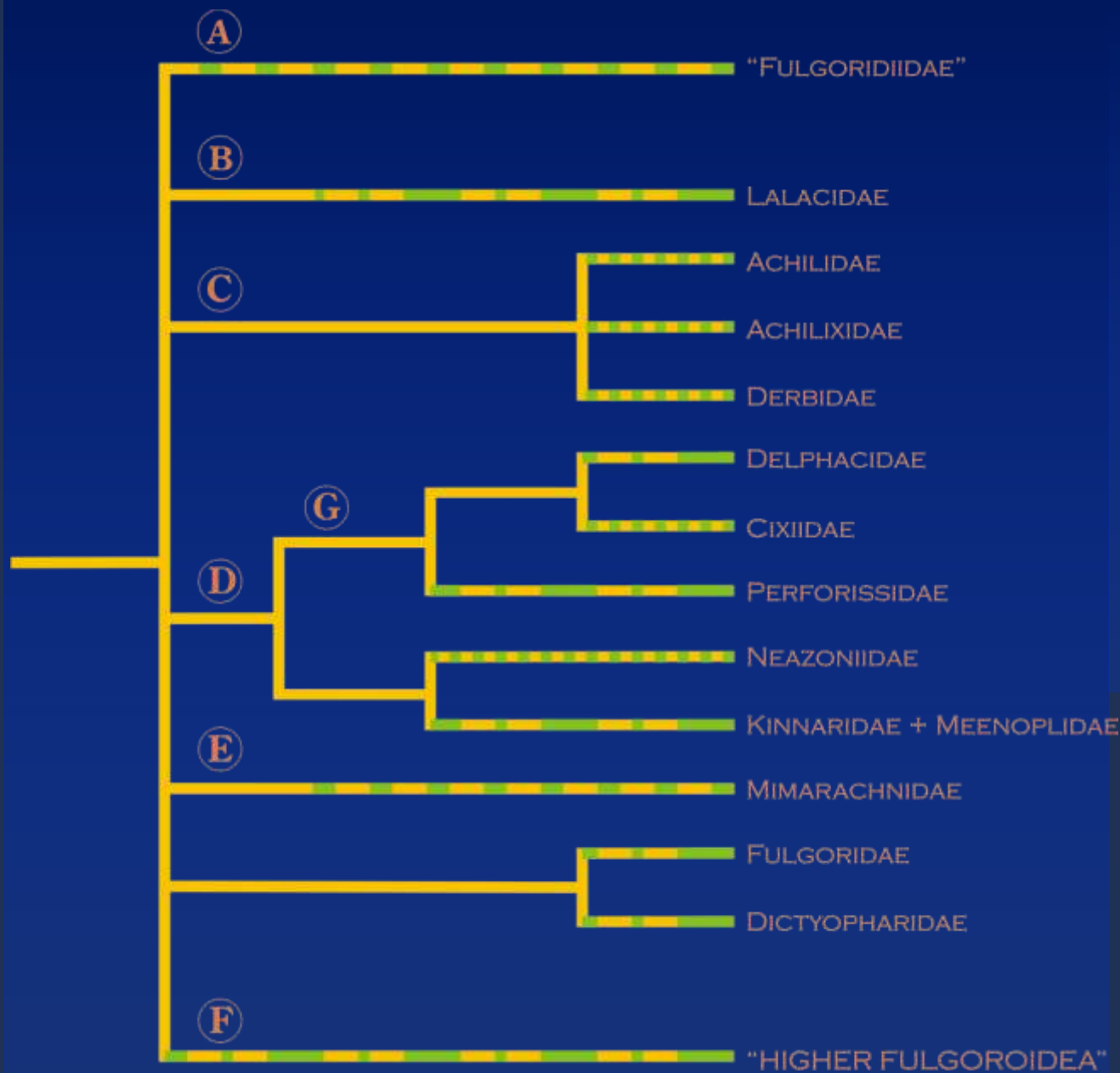
Conifers
(macrophyllous)



Ferns



Sphenopsids



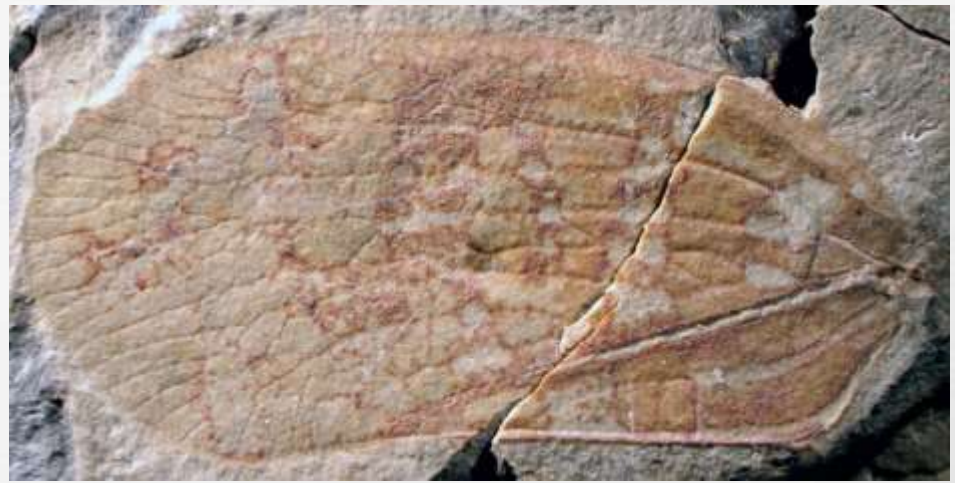
A – "Fulgoridiidae" - a paraphyletic unit, ancestral for other Fulgoroidea;
 B – Lalacidae – one of the "short living" families from the times of Mid-Cretaceous biotic turnover;
 C – Monophyletic clade with not-monophyletic families;
 D – "Cixiidae-like" groups, monophyly is weakly supported;
 E – Placement of Mimarachnidae is tentative;
 F – So called "higher Fulgoroidea" seems to be not monophyletic clade;
 G - Cixiidae could be not monophyletic.

Jurassic Fulgoromorpha – variety, unity and ancestry for modern planthoppers

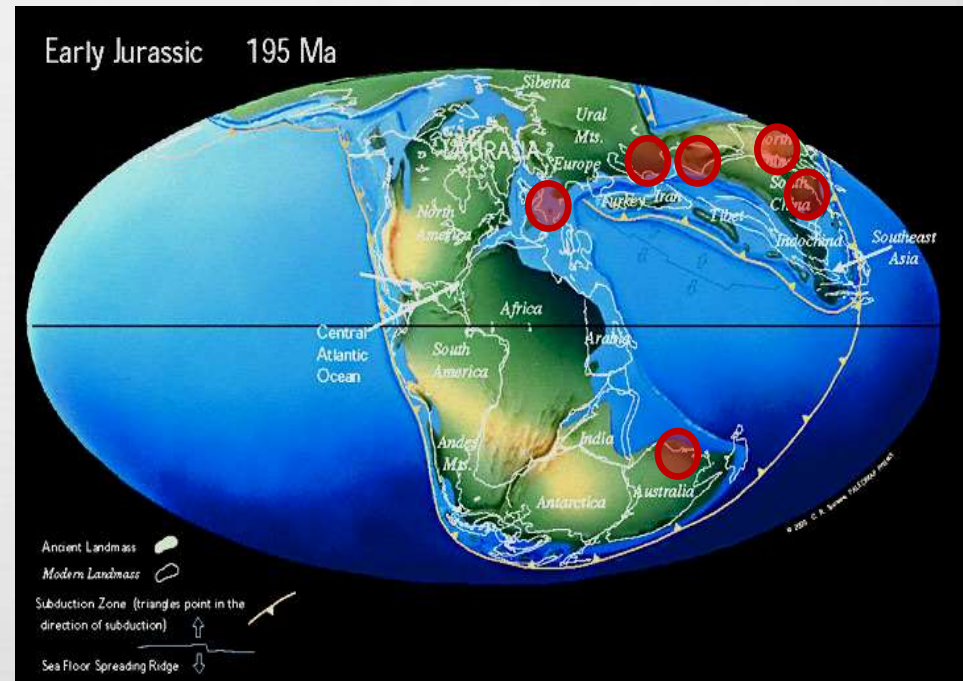


Fulgoridiidae

Auliezidium, *Cixiites*, *Compactofulgoridium*,
Conofulgoridium, *Eofulgoridium*,
Fulgoridiella, *Fulgoridium*, *Fulgoridulum*,
Fulgoropsis, *Margaroptilon*, *Metafulgoridium*,
Parafulgoridium, *Procercofulgoridium*,
Productofulgoridium, *Tetragonidium*,
Valvifulgoria



Qiyangiricaniidae: *Qiyangiricania cesta*



Jurassic Palaeontinidae – spectacular success



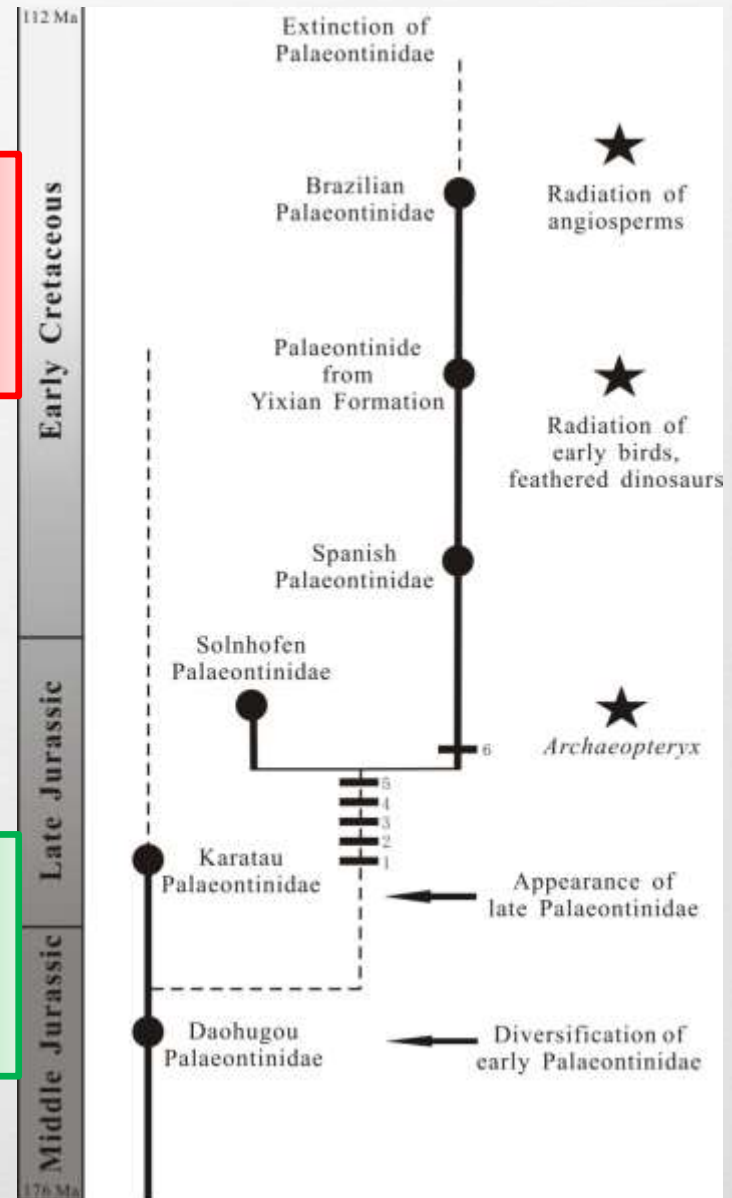
Palaeontinoidea Handlirsch, 1906

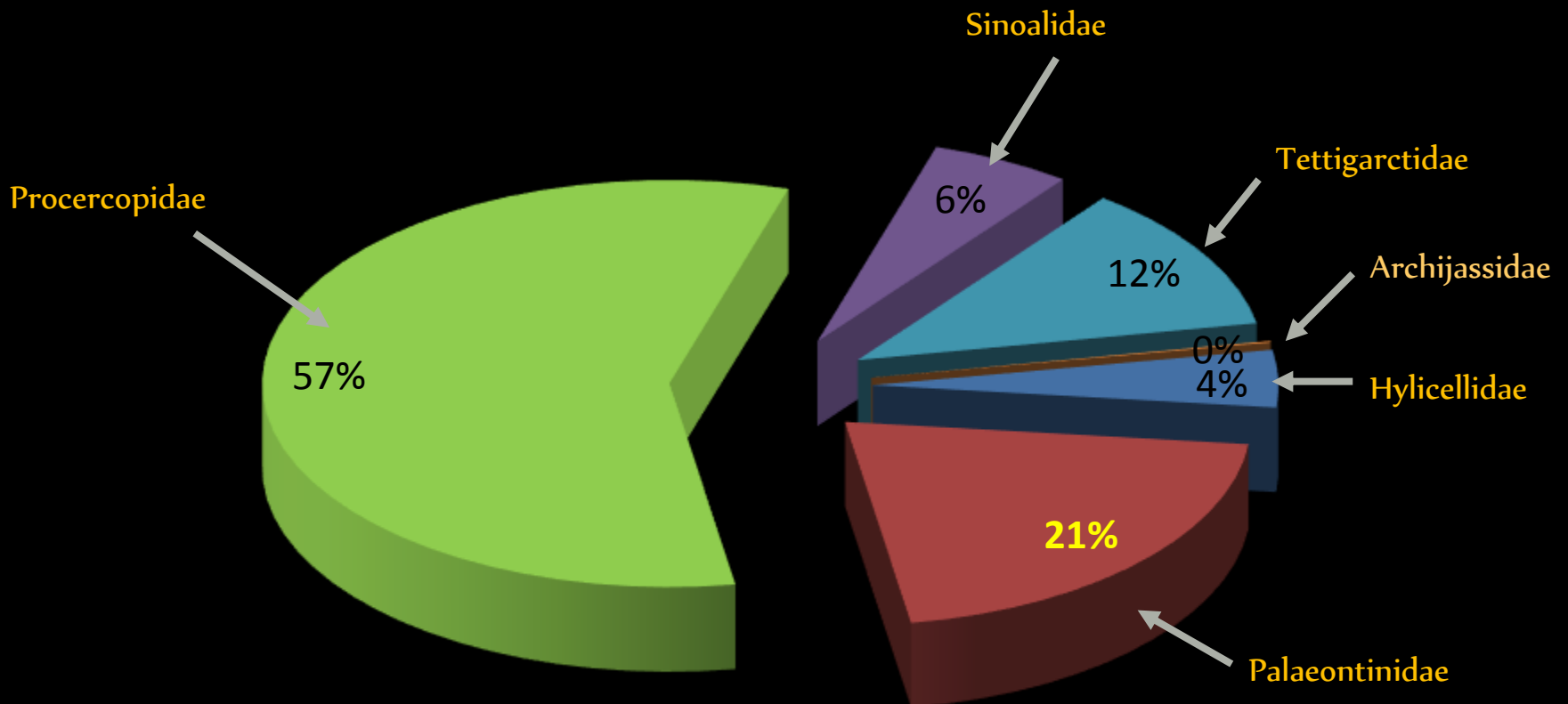


11 genera



22 genera



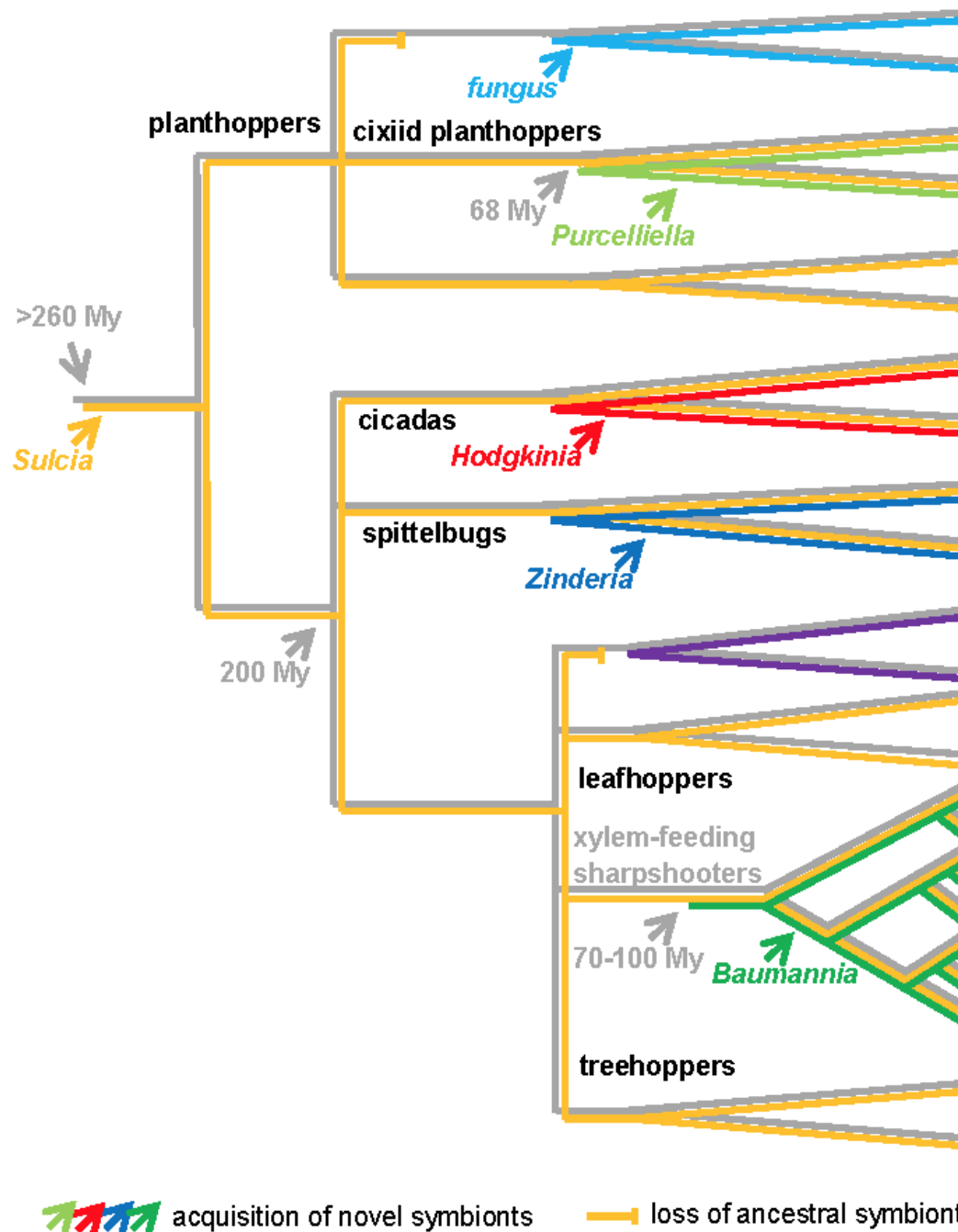


Jurassic reign of Procercopidae

Acquisition of symbionts among Euhemiptera

Euhemiptera

- known since the Carboniferous
- variable symbiotic systems
- phloem-feeding
- xylem-feeding (various adaptations)
- mesophyll-feeding (loss of symbionts)
- predators
- blood-feeders
- secondary plant-feeding



Episode 6



CRETACEOUS BIOTIC
RE-ORGANIZATION AND
CAINOZOIC DIVERSIFICATION

— underlined sub-families contain species associated with coniferous hosts

Host alternation

Families showing characters considered as plesiomorphous

Radiation on gymnosperms

Radiation on ancestors of modern angiosperms and conifers

Mid-Cretaceous Terrestrial Revolution

Ancestors feeding on early rosaceae?

Most species-rich subfamily (2500 species)

Phyloxeridae

Adelgidae

Neophyllaphidinae

Mindarinae

Eriosomatinae

Erisomatini
Pemphigini¹
Fordini^{2,3}

Thelaxinae

Anoeciinae

Hormaphidinae

Pterastheniinae

Phyllaphidinae

Saltusaphidinae

Parachaitophorinae

Neuquenaphidinae

Myzocallidinae

Phloeomyzinae

Macropodaphidinae

Lizeriinae

Tamaliinae

Israelaphidinae

Taiwanaphidinae

Greenideinae

Aiceoninae

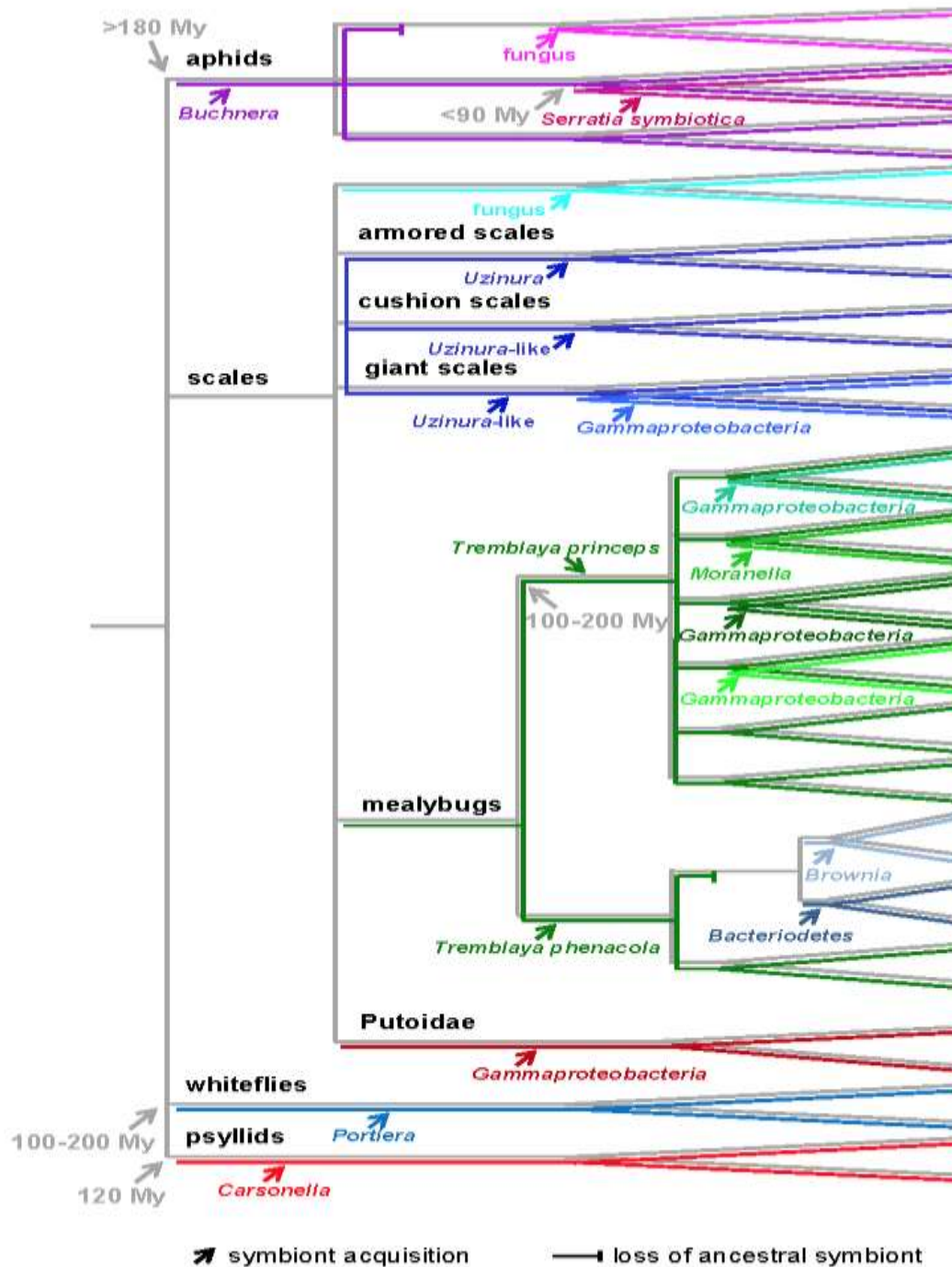
Chaitophorinae

Drepanosiphinae

Lachninae⁴

Aphidinae Pterocommatinae⁵





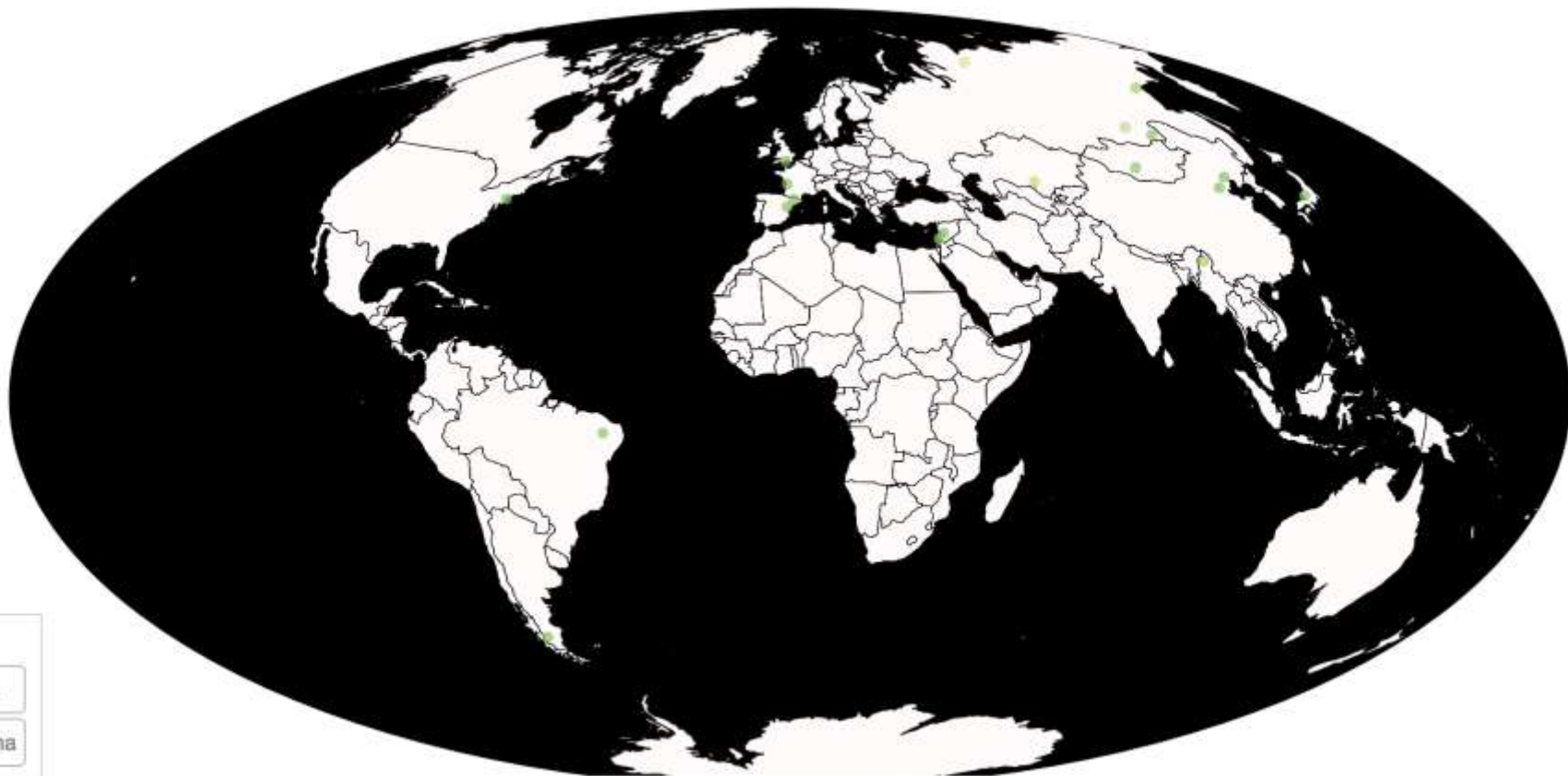
Multiple acquisitions and losses of symbionts among Sternorrhyncha

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Filters

☒ Cretaceous

☒ Fulgoromorpha



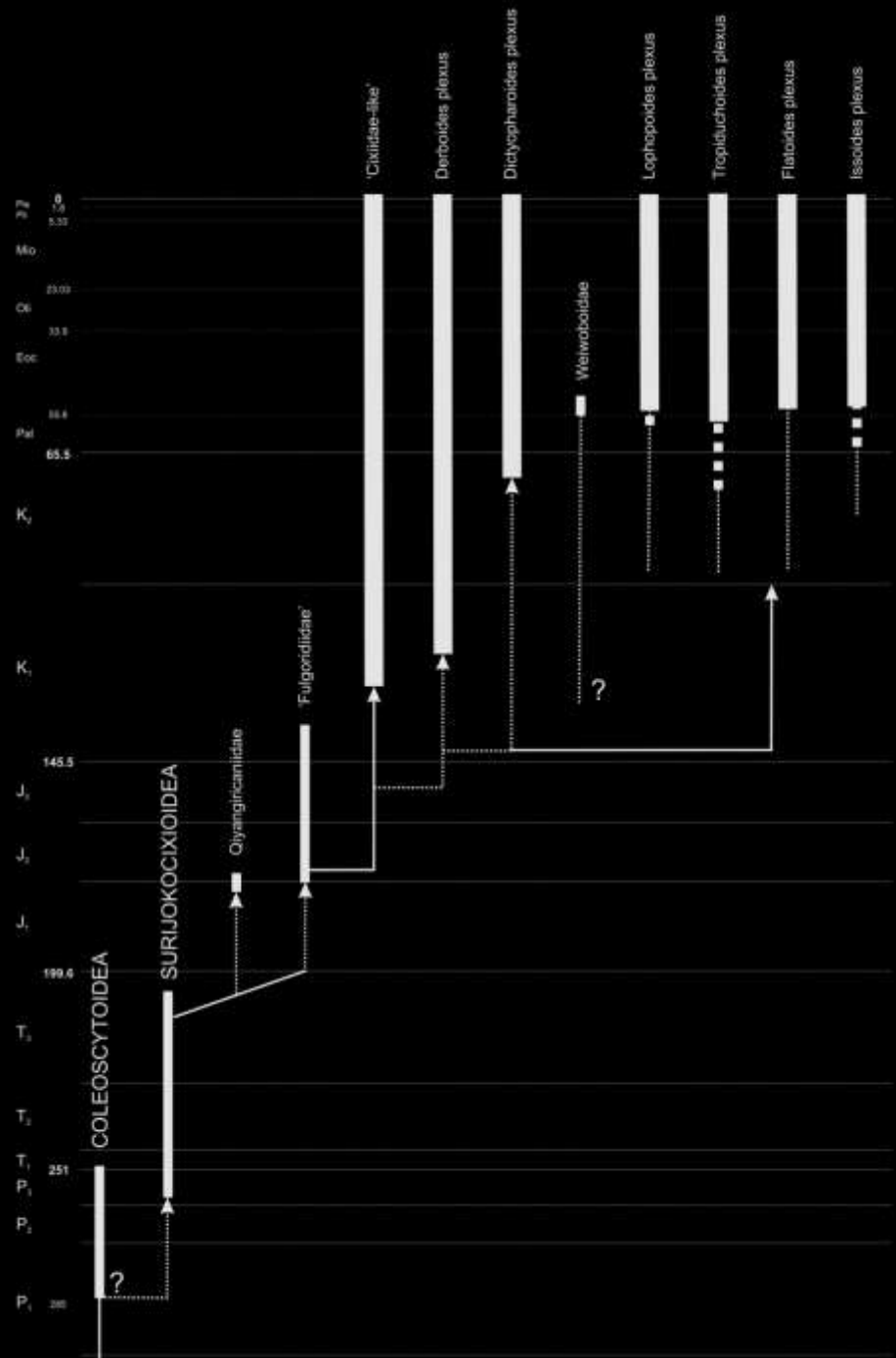
Mid-Cretaceous reorganization of biosphere

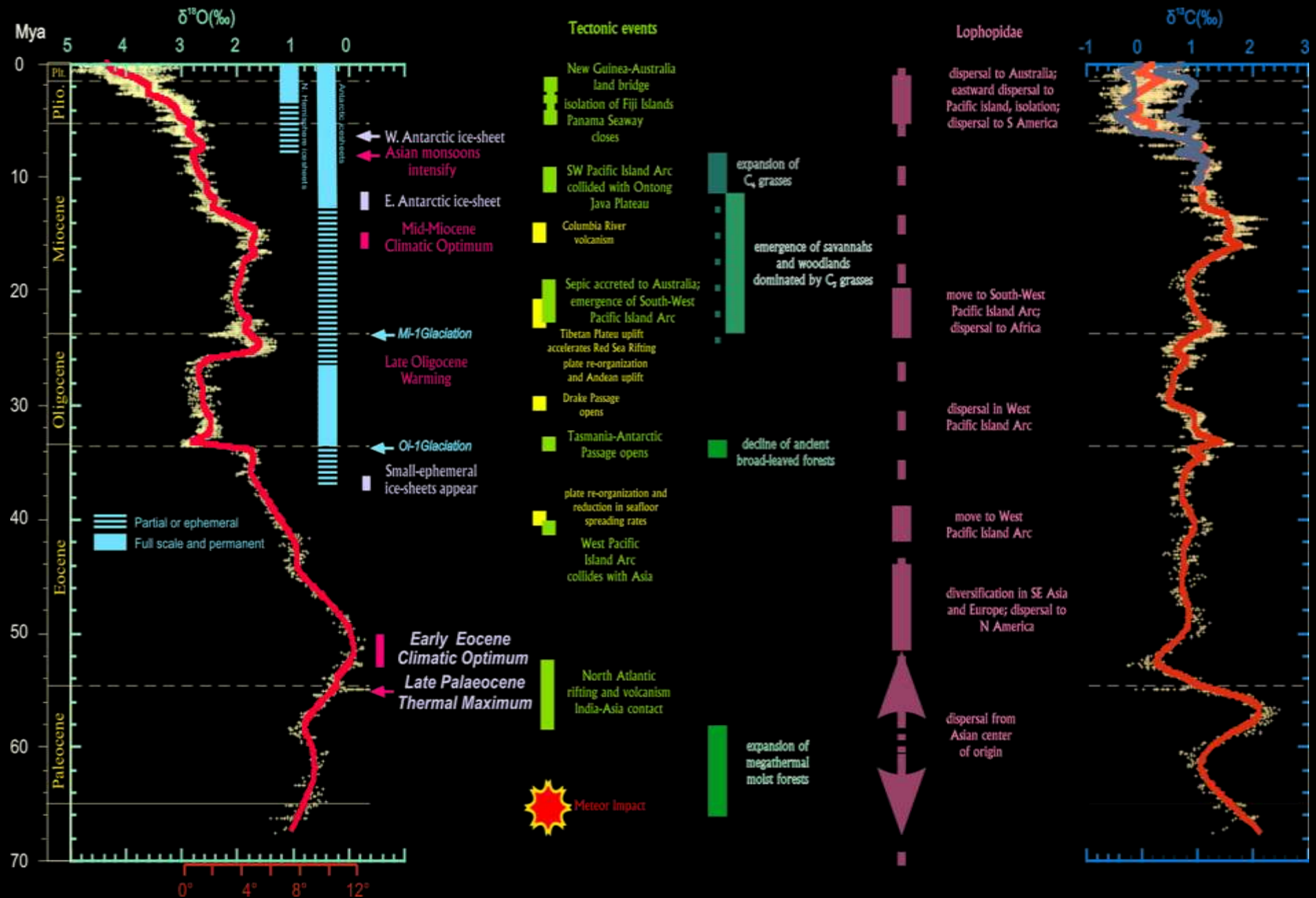
- ◆ extinction of Paleozoic and many Mesozoic groups (e.g. Palaeontinidae, some Fulgoroidea, some Sternorrhyncha)
- ◆ modern groups appear and diversify due to new host plants (angiosperms) radiation
- ◆ new endosymbiotic relationships? (as answer to host plant challenges)
- ◆ climatic changes – drying and cooling in Neogene
- ◆ grassland expansion and grassland related lineages radiations



Fulgoromorpha: Fulgoroidea

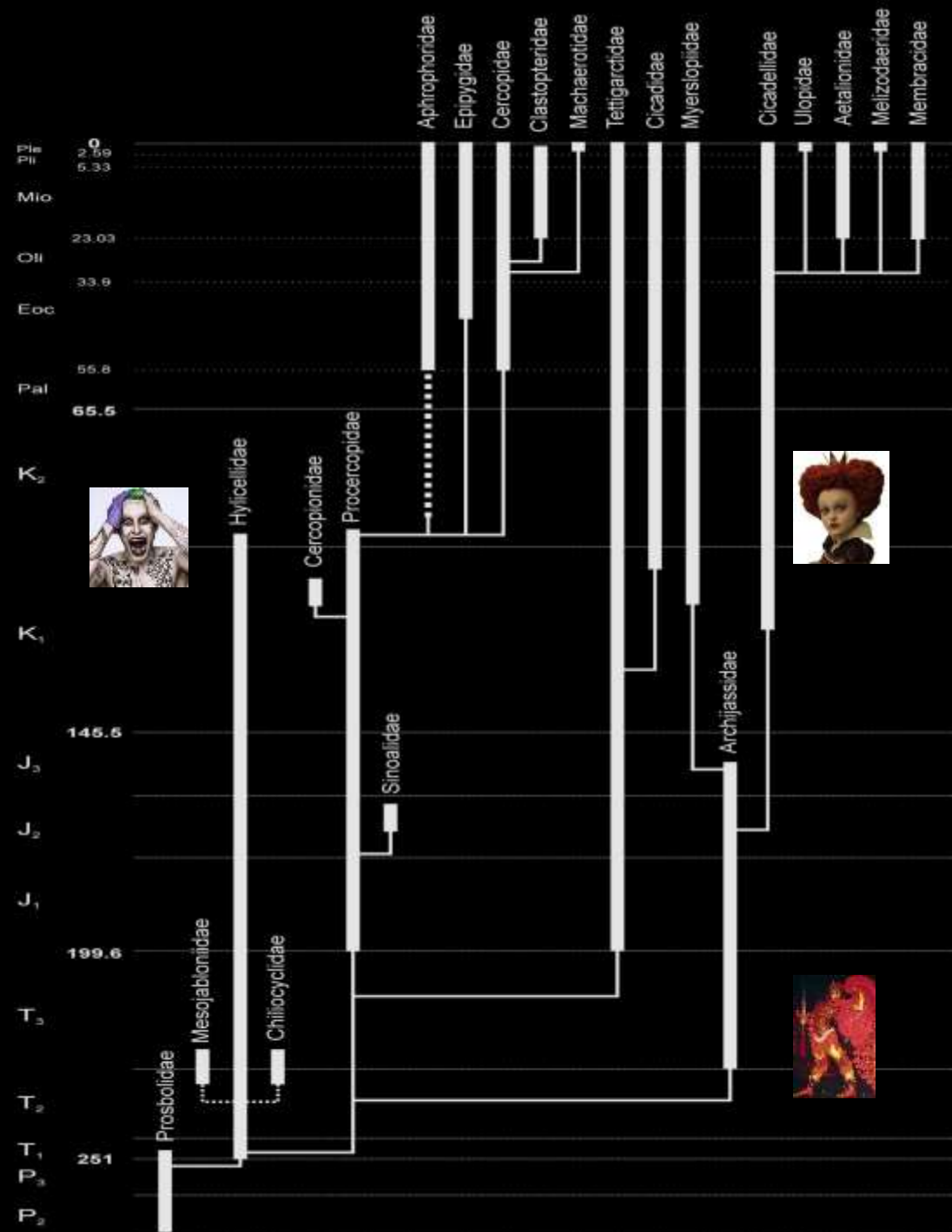
- base of tegmen covered with enlarged tegula;
- tegminal basicubital triangle shortened;
- head with carinae;
- mesonotum with longitudinal carinae;
- metanotum with longitudinal carinae;
- 2nd and 3rd coxae stretched out;
- 2nd and 3rd coxae separated basally, remaining contiguous apically;
- nymphal 'gears'?
- jumping, free living nymphs





Clypeata

- ❖ The only surviving group of Cicadomorpha, present in the Recent fauna
- ❖ The recent groups are descendants of the Hylcelloidea
- ❖ Modern Cercopoidea diversified in the late Cretaceous
- ❖ Modern Cicadoidea diversified in the Cenozoic
- ❖ Membracoidea diversified in the late Jurassic/early Cretaceous
- ❖ Explosive diversification of Cicadellidae related to floristic and climatic changes in the Palaeogene
- ❖ Membracidae could be neotenous offshot of Cicadellidae, with origins influenced by the global cooling and drying events in the Oligocene/Miocene







The Red Queen Hypothesis suggests that continuing adaptation is needed in order for a species to survive and thrive. Everything else surrounding the species- the environment and the species' competitors – is changing. In one use of this hypothesis, every individual becomes an experiment. Every individual must find the way by adapting to changes.

The Court Jester Hypothesis suggests that environmental factors provide the drive for evolution in species. Big examples such as meteors and storms are often used to explain these environmental factors, but even day-to-day things like temperature can initiate a species to change or adapt.

Interestingly, the Red Queen and the Court Jester can work together. They explain different parts of a complex whole and they don't necessarily step on each other's toes.

...but there is another player in this evolutionary game - **The Red King**

Coevolution of two species is typically thought to favour the evolution of faster evolutionary rates helping a species keep ahead in **the Red Queen** race. In contrast, if species are in a mutualistic relationship, it was proposed that **the Red King** effect may act, where it can be beneficial to evolve slower than the mutualistic species. **The Red King** hypothesis proposes that the species which evolves slower can gain a larger share of the benefits.



How the Red King effect is involved and how it has influenced the evolutionary traits of the Hemiptera – this question remains open. However, the Hemiptera present number of internal symbiotic relationships as well as symbiotic relationships with external partners. Hence, this effect should not be neglected in reconstruction of the evolutionary history of the Hemiptera.

However, this is fascination and frustration of research resolving the long-standing puzzle of evolution.

Thank you!



Credits: Lewis Carroll, Leigh Van Valen, Anthony D. Barnosky, Carl T. Bergstrom, Michael Lachmann, Michael Benton, Helen Bonham-Carter, Jack Nicholson, Heath Ledger, Jared Leto, Tim Burton, Chris Nolan, David Ayer, Charles Darwin, Alfred R. Wallace, Claude Combes, Richard Dawkins, David M. Raup, Steven M. Stanley, Jan Koteja, Elżbieta Sontag, Barbara Kosmowska-Ceranowicz, Róża Kulicka, Karol Sabbath, Jerzy Dzik, Zofia Pleń, International Commission on Zoological Nomenclature, International Commission on Stratigraphy, Adam Stroiński, Ryszard Szadziwski, Karol Szawaryn, Teresa Szklarzewicz, Anna Michalik, Aleksandra Urbanek, Elena R. Toenschhoff, Nancy A. Moran, Gordon Bennett, James L. Rainford, Peter J. Mayhew, Peter A. Allison, David J. Bottjer, Peter Ax, Alexandr P. Rasnitsyn, Alexandr G. Ponomarenko, Alexandr F. Emeljanov, Dimitri E. Shcherbakov, Kiril Yu. Eskov, Vladimir V. Zherikhin, Rolf G. Beutel, Viktor Hartung, Bo Wang, Łukasz Rostkowski, Anja Orthodox, Maynard J. Keenan, Alison Goldfrapp, Will Gregory, Max Richter, Mark Hollis, Aleksandra Kaczkowska, Derek E.G. Briggs, Eric Buffetaut, Dave Penney, Andre J. Ross, Dany Azar, Andre Nel, Nikita Yu. Kluge and many, many others....

The talk presents unpublished results and interpretations

*Episodes in history of
the Hemiptera*