THE FOSSIL RECORD OF STERNORRHYNCHA (HEMIPTERA)

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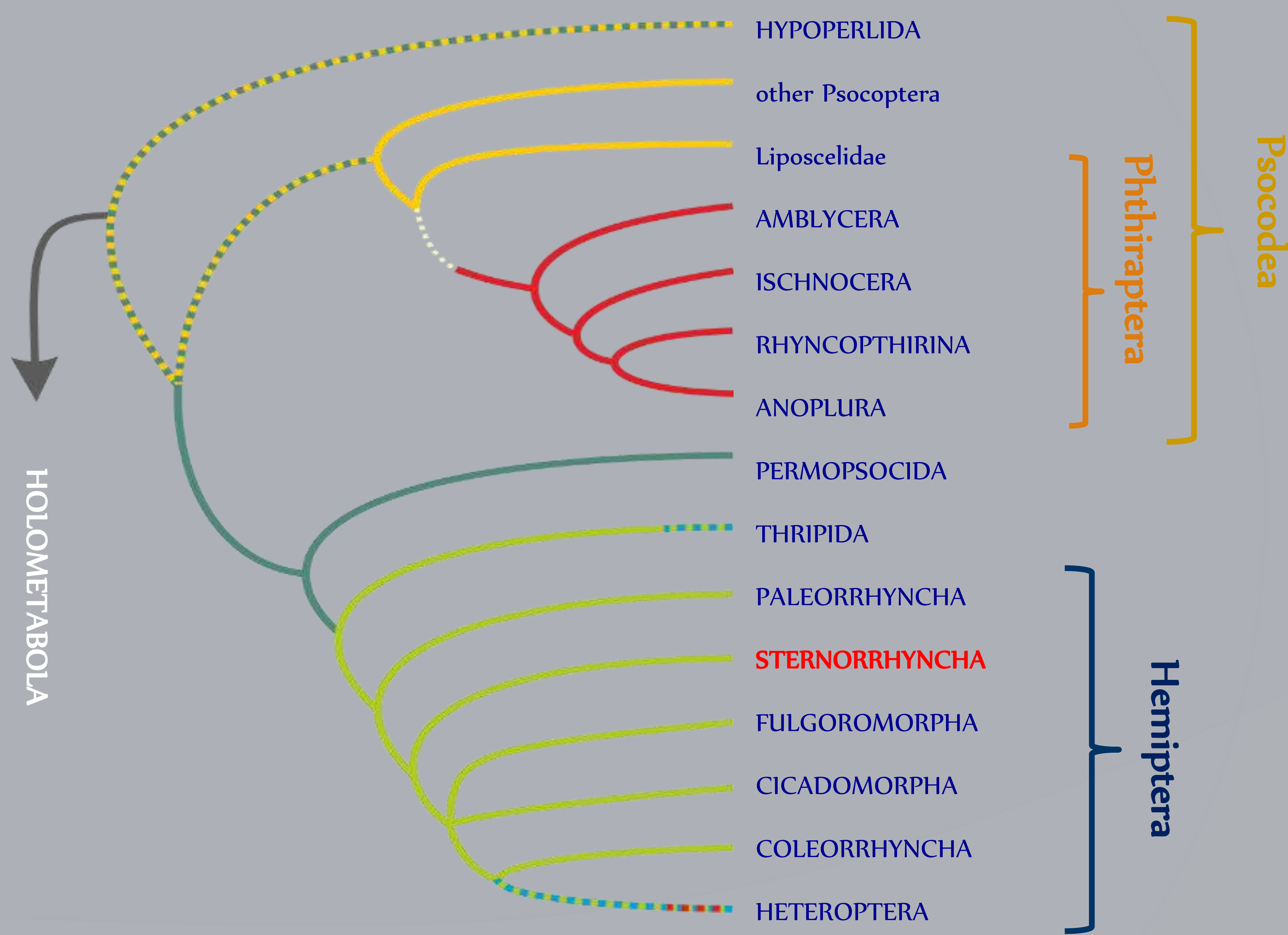
535: Symposium: Synthesis in Sternorrhyncha Systematics


HYPOPERLIDA
other Psocoptera
Liposcelidae
AMBLYCERA
ISCHNOCERA
RHYNCOPTHIRINA
ANOPLURA
PERMOPSOCIDA
THRIPIDA
PALEORRHYNCHA
STERNORRHYNCHA
FULGOROMORPHA
CICADOMORPHA
COLEORRHYNCHA
HETEROPTERA
Psocodea
Phthiraptera
Hemiptera
HOLOMETABOLA

Sternorrhyncha questions

- Where to search for sternorrhynchan ancestors?
- What constitutes a sternorrhynchan insect?

The recent morphological disparity and biodiversity is enormous, then which characters can be used for the fossils?

- Which is the oldest Sternorrhyncha?

The questions where and when the splitting of Sternorrhyncha from hemipteran stock took place are not fully answered.

INTERNATIONAL CHRONOSTRATIGRAPHIC CHART

IUGS

www.stratigraphy.org — International Commission on Stratigraphy — v 2016/04

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	numerical age (Ma)
Phanerozoic	Cenozoic	Quaternary			present
			Holocene		0.0117
			Pleistocene	Upper	0.126
				Middle	0.781
				Calabrian	1.80
				Gelasian	2.58
		Neogene	Pliocene	Piacenzian	3.600
				Zanclean	5.333
			Miocene	Messinian	7.246
				Tortonian	11.63
				Serravallian	13.82
				Langhian	15.97
				Burdigalian	20.44
				Aquitanian	23.03
		Paleogene	Oligocene	Chattian	28.1
				Rupelian	33.9
			Eocene	Priabonian	37.8
				Bartonian	41.2
				Lutetian	47.8
				Ypresian	56.0
			Paleocene	Thanetian	59.2
				Selandian	61.6
				Danian	66.0
	Mesozoic	Cretaceous	Upper	Maastrichtian	72.1 ±0.2
				Campanian	83.6 ±0.2
				Santonian	86.3 ±0.5
				Coniacian	89.8 ±0.3
				Turonian	93.9
				Cenomanian	100.5
			Lower	Albian	~ 113.0
				Aptian	~ 125.0
				Barremian	~ 129.4
				Hauterivian	~ 132.9
				Valanginian	~ 139.8
				Berriasian	~ 145.0

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	numerical age (Ma)
Phanerozoic	Mesozoic	Jurassic			~ 145.0
			Upper	Tithonian	152.1 ±0.9
				Kimmeridgian	157.3 ±1.0
				Oxfordian	163.5 ±1.0
			Middle	Callovian	166.1 ±1.2
				Bathonian	168.3 ±1.3
				Bajocian	170.3 ±1.4
				Aalenian	174.1 ±1.0
			Lower	Toarcian	182.7 ±0.7
				Pliensbachian	190.8 ±1.0
				Sinemurian	199.3 ±0.3
				Hettangian	201.3 ±0.2
		Triassic	Upper	Rhaetian	~ 208.5
				Norian	~ 227
				Carnian	~ 237
			Middle	Ladinian	~ 242
				Anisian	247.2
			Lower	Olenekian	251.2
				Induan	252.17 ±0.06
	Paleozoic	Permian	Lopingian	Changhsingian	254.14 ±0.07
				Wuchiapingian	259.8 ±0.4
			Guadalupian	Capitanian	265.1 ±0.4
				Wordian	268.8 ±0.5
				Roadian	272.3 ±0.5
			Cisuralian	Kungurian	283.5 ±0.6
				Artinskian	290.1 ±0.26
				Sakmarian	295.0 ±0.18
				Asselian	298.9 ±0.15
		Carboniferous — Pennsylvanian	Upper	Gzhelian	303.7 ±0.1
				Kasimovian	307.0 ±0.1
			Middle	Moscovian	315.2 ±0.2
			Lower	Bashkirian	323.2 ±0.4
		Carboniferous — Mississippian	Upper	Serpukhovian	330.9 ±0.2
			Middle	Visean	346.7 ±0.4
			Lower	Tournaisian	358.9 ±0.4

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	numerical age (Ma)
Phanerozoic	Paleozoic	Devonian			358.9 ± 0.4
			Upper	Famennian	372.2 ±1.6
				Frasnian	382.7 ±1.6
			Middle	Givetian	387.7 ±0.8
				Eifelian	393.3 ±1.2
			Lower	Emsian	407.6 ±2.6
				Pragian	410.8 ±2.8
				Lochkovian	419.2 ±3.2
		Silurian	Pridoli		423.0 ±2.3
			Ludlow	Ludfordian	425.6 ±0.9
				Gorstian	427.4 ±0.5
			Wenlock	Homerian	430.5 ±0.7
				Sheinwoodian	433.4 ±0.8
			Llandovery	Telychian	438.5 ±1.1
				Aeronian	440.8 ±1.2
				Rhuddanian	443.8 ±1.5
		Ordovician	Upper	Hirnantian	445.2 ±1.4
				Katian	453.0 ±0.7
				Sandbian	458.4 ±0.9
			Middle	Darriwilian	467.3 ±1.1
				Dapingian	470.0 ±1.4
			Lower	Floian	477.7 ±1.4
				Tremadocian	485.4 ±1.9
		Cambrian	Furongian	*Stage 10*	~ 489.5
				Jiangshanian	~ 494
				Paibian	~ 497
			Series 3	Guzhangian	~ 500.5
				Drumian	~ 504.5
				Stage 5	~ 509
			Series 2	*Stage 4*	~ 514
				Stage 3	~ 521
			Terreneuvian	*Stage 2*	~ 529
				Fortunian	541.0 ±1.0

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

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 uni ts 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.ccgm.org)

CCGM CGMW

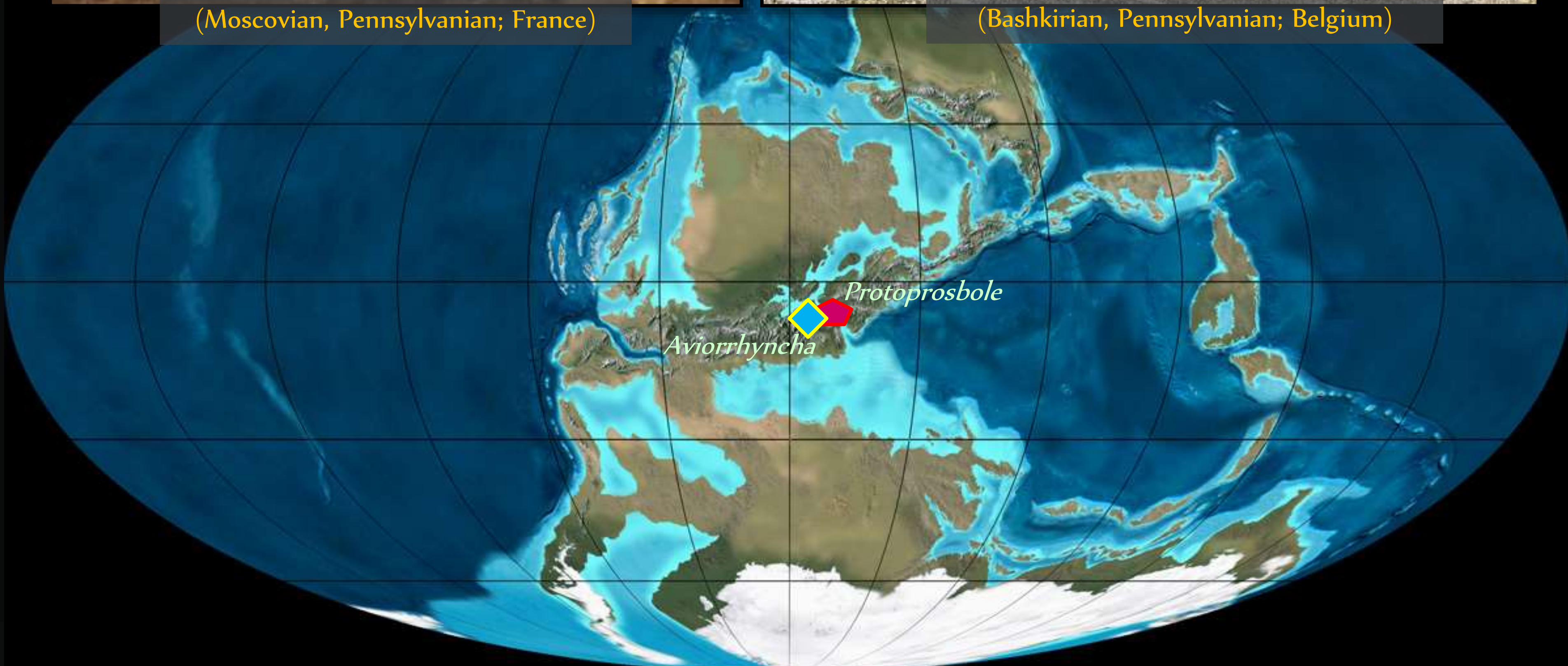
Chart drafted by K.M. Cohen, S.C. Finney, P.L. Gibbard

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

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

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



Suborder Paleorrhyncha

Fam: Archescytinidae

= Permopsylliidae

= Lithoscytinidae

= Maueriidae

= Permoscytinopsidae

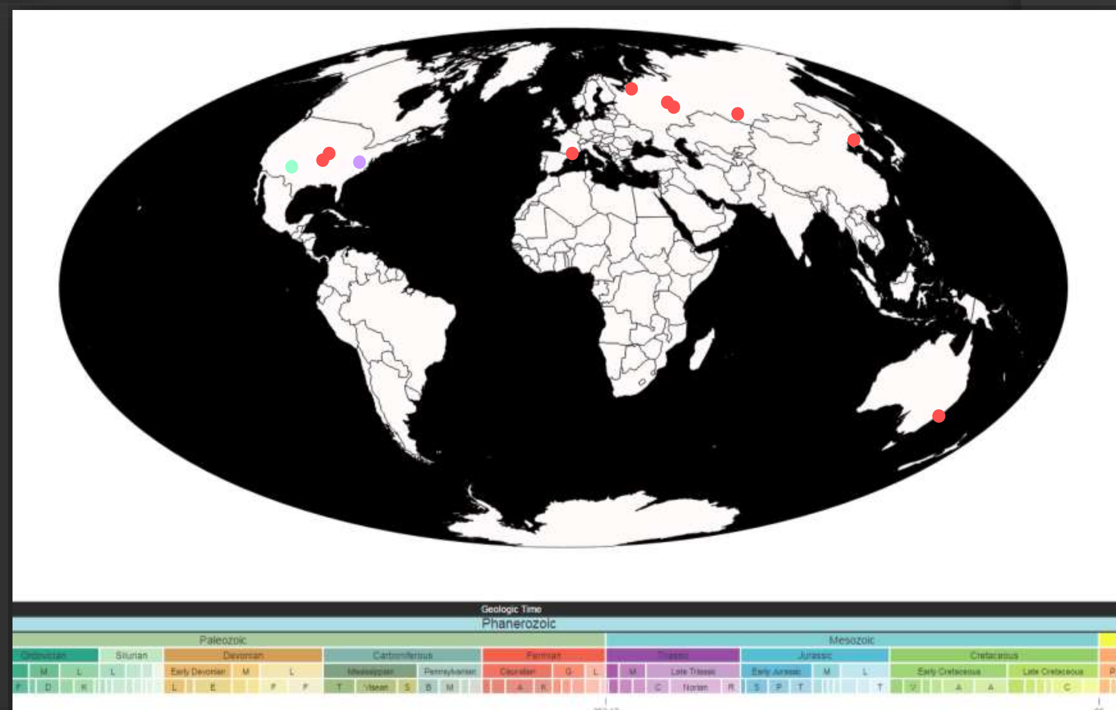
= Uraloscytinidae

= Maripsocidae

= Kaltanaphididae

There is a considerable diversity of Permian hemipterans, but their relationships are obscure.

The supposed ancestors of the Sternorrhyncha are among the members of the suborder Paleorrhyncha.

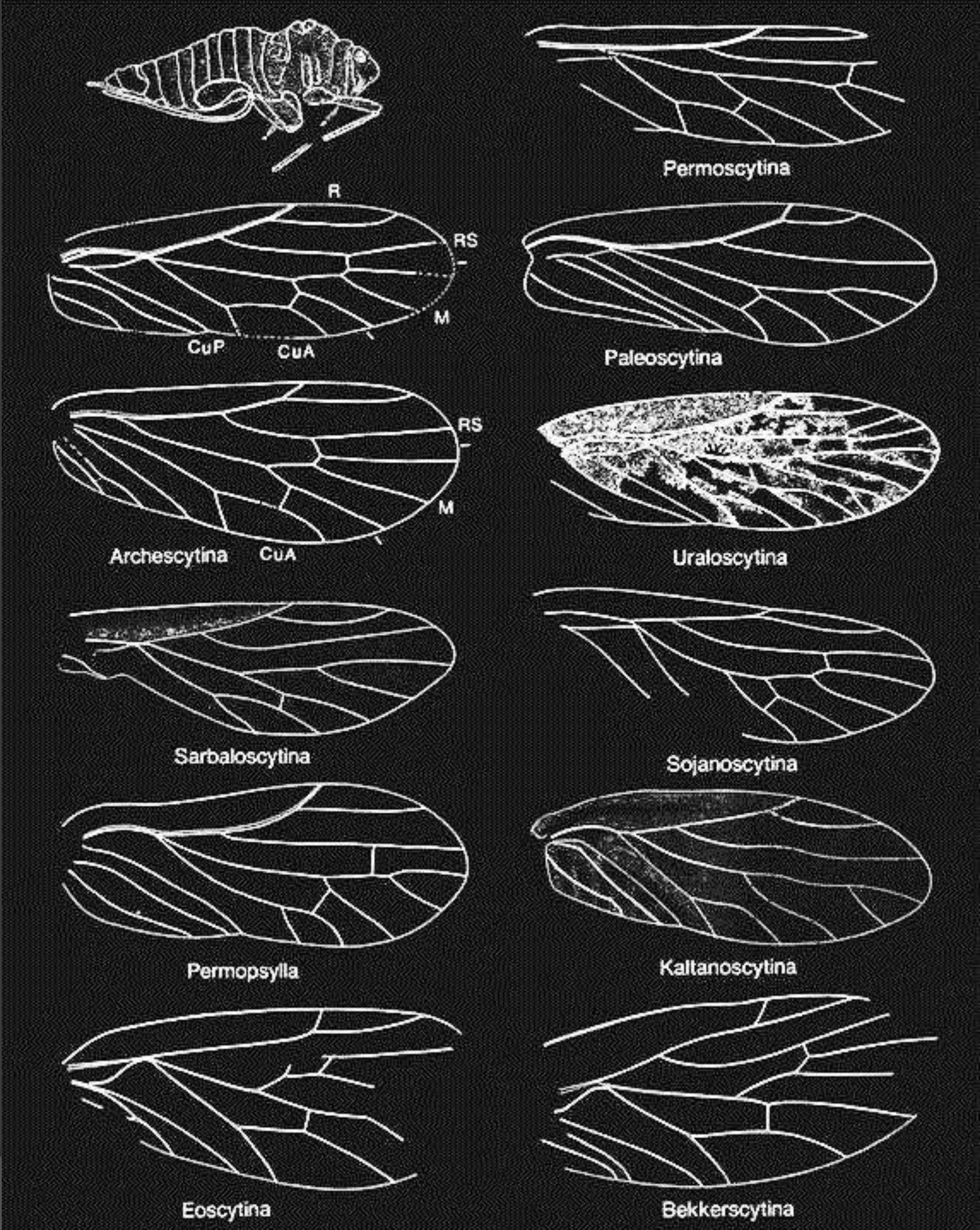


Where to search for Sternorrhyncha ancestors?

Paleorrhyncha

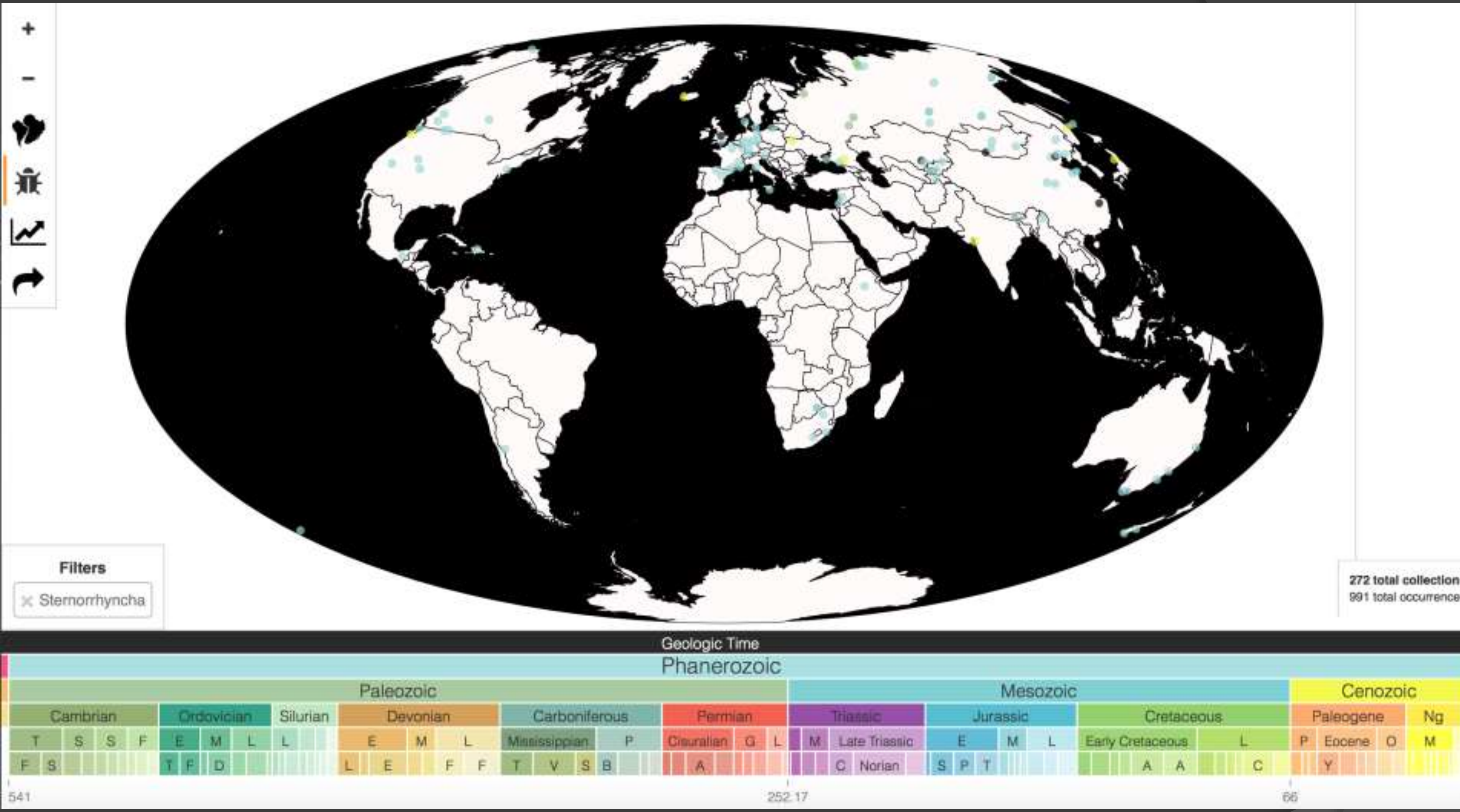
This group is a paraphyletic assemblage, ranging from the late Carboniferous (300 mya) to late Permian (270 mya).

- smaller size
- homonomic venation of forewings and hind wings
- antennae 10-segmented with rhinaria
- probably gall-making
- trophic relationships with seed ferns and early gymnosperms



Paleorrhyncha display several morphological specializations, e.g. variously formed ovipositors from short needle-like to very long, and forming a coil under the body. Also the placement of the rostrum base is variable. On the other hand, they show some sternorrhynchous characters, i.e. smaller size, antennae with rhinaria, and relatively simple venation.

Rasnitsyn & Quicke (2002)



The fossil record of the Sternorrhyncha stretches back to the Permian (270 mya); most of the fossil sites are distributed in the northern hemisphere; and only a few sites are located in the southern hemisphere.

Where to search for sternorrhynchan ancestors?

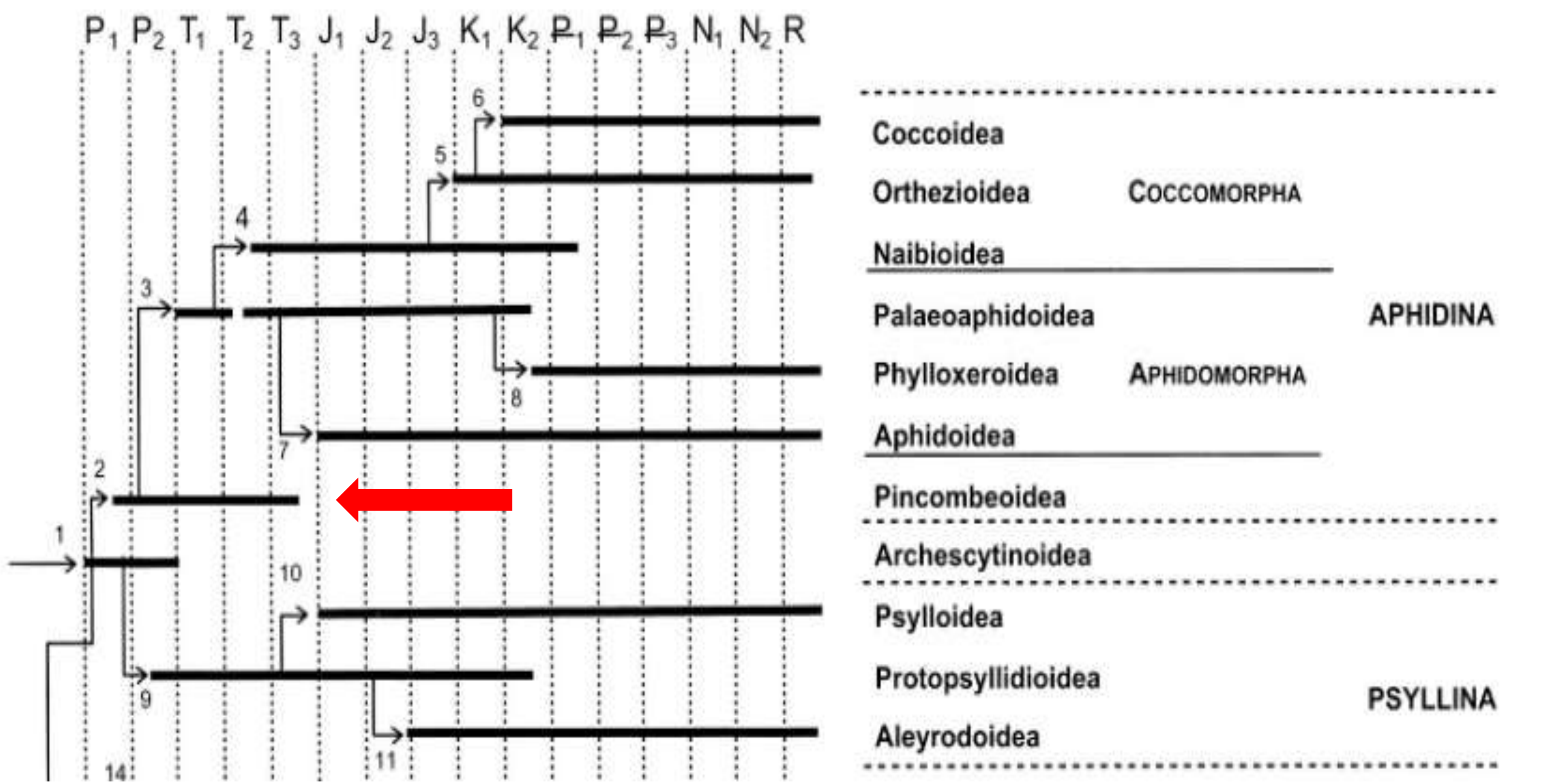
Sternorrhyncha

- Earliest Sternorrhyncha are closely related to the Paleorrhyncha (ancestral or sister-group relationship to be revealed)
- According to the fossil record, the lineage Pincombeomorpha + Aphidomorpha separated earlier than Psylloidea + Aleyrodoidea
- exclusively plant sap-feeders (phloem feeders)
- underwent morphological and behavioral differentiation in the Permian
- have the first major radiation in the Triassic (250–200 mya)
- the second in the Late Cretaceous (100–65 mya)




What constitutes a sternorrhynchan insect ?

First separation of Sternorrhyncha took place in the Permian (250 mya), when the infraorders Pincombeomorpha and Aphidomorpha appeared. Pincombeomorpha, with three families occur in the Permian to the Late Triassic (about 270–200 mya).



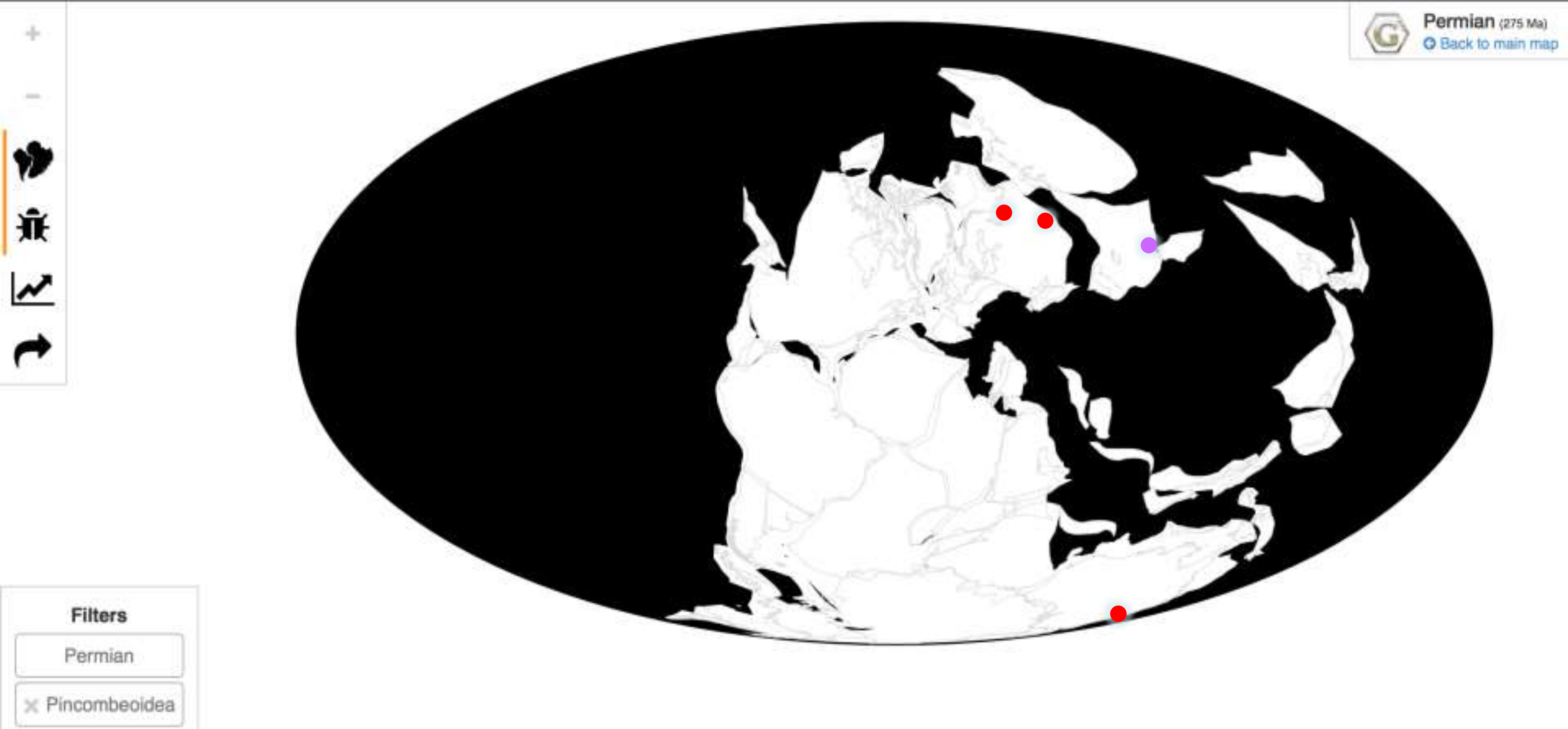
Rasnitsyn & Quicke (2002)

Pincombeomorpha

Their characters are the forewing with the radius posterior vein (RP) originating well before the pterostigma, convex up to the nodal line and concave beyond it; nodal line crossing RP near base; median vein (M) and cubitus anterior vein (CuA) forming a short common stalk; claval vein(s) remote from posterior margin.

Pincombea sp.
Upper Permian, Australia

Simulaphis shaposhnikovi Shcherbakov, 2007
Upper Permian, Australia



During the Permian (300-250 mya), Pincombeomorpha were present in both hemispheres, but from the Triassic they are only known from the northern hemisphere.

Pincombeidae (Permian-Triassic)

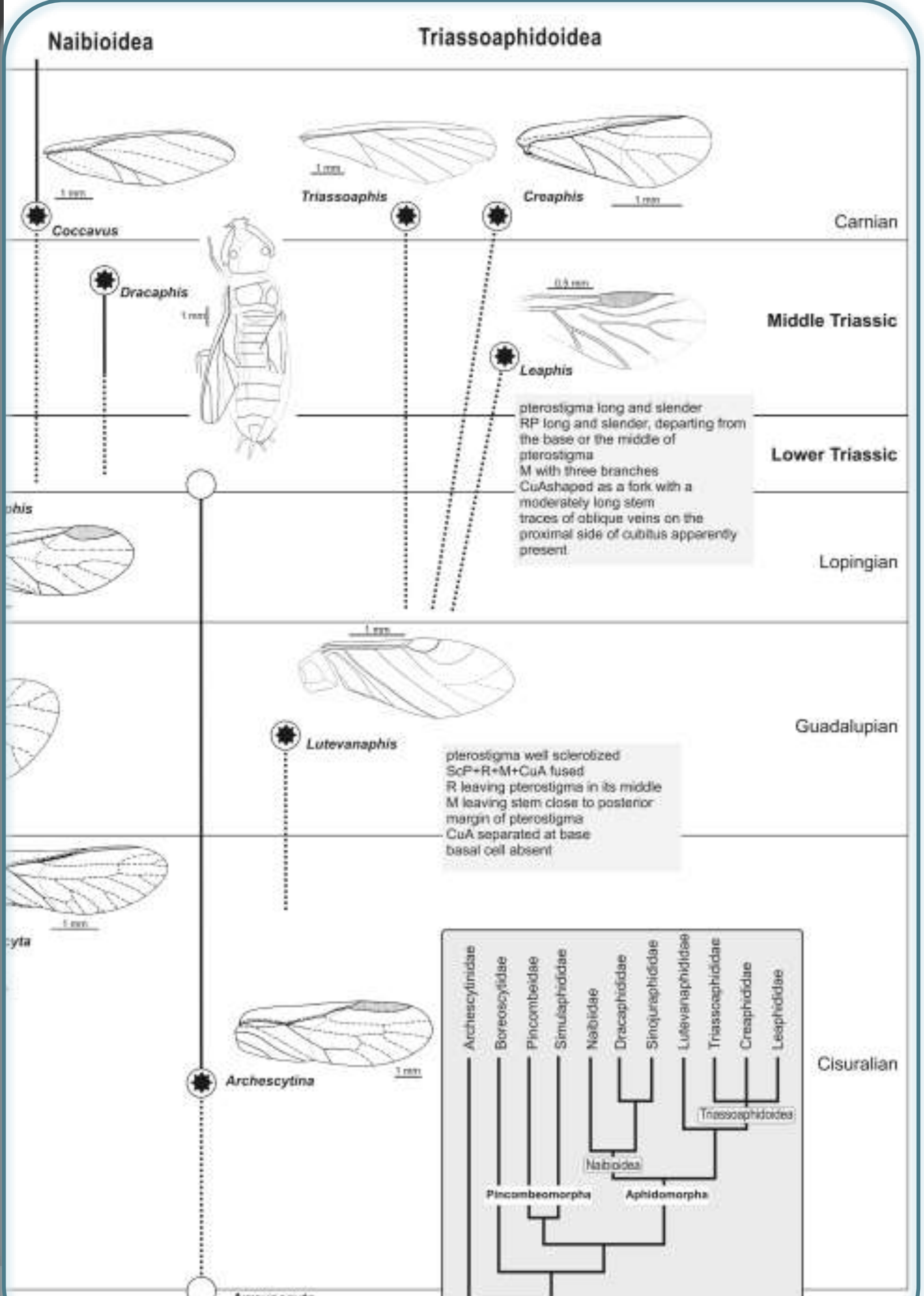
Simulaphididae (Permian)

Boreoscytidae (Permian)

- Evolutionary histories of each extant sternorrhynchan lineage – aphids, coccids, psyllids and whiteflies are far from complete.
- They are rarely fossilized because they have small and delicate bodies, and the known fossils are preserved mostly in Cretaceous and Cenozoic ambers.
- Next part I will briefly introduce the history of these lineages.

The early evolution of aphids

(Aphidomorpha)

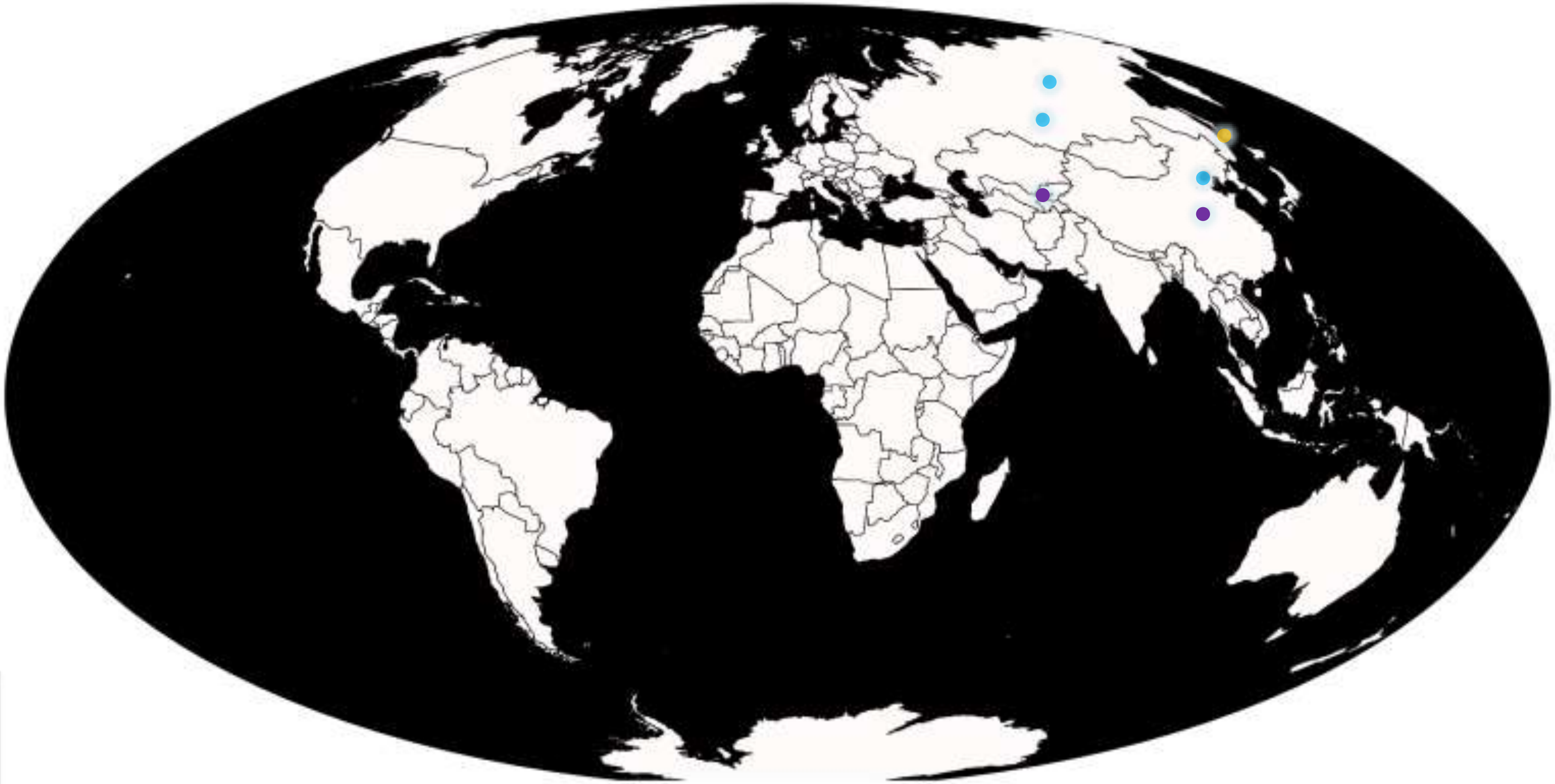


Szwedo *et al.* (2015)

Aphidomorpha occurs in the Permian, is represented by one species. After the great Permian/Triassic extinction event, aphids rebuilt its diversity with two superfamilies, Naibioidea and Triassoaphidioidea.

Triassic aphids

- wing shapes from oval to triangular
- reduction of basal cell
- reduction of venation
- loss of vein M connection with stem
- reduction of costal area and anal lobe (clavus)

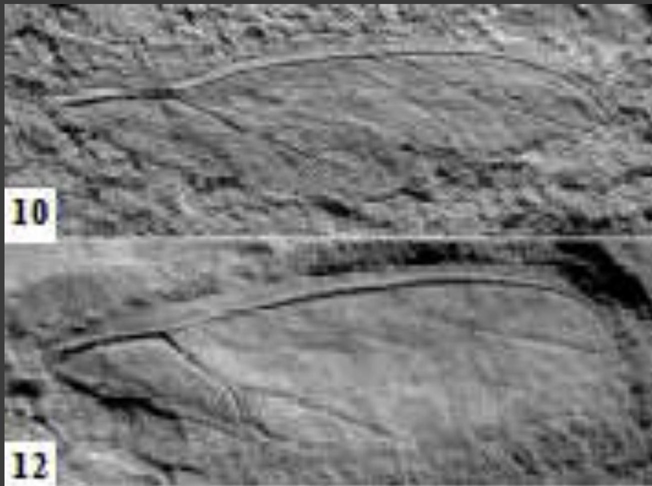


Naibioidea with three families are known from the Triassic to the Eocene (240–50 mya). They are only reported from the northern hemisphere:

Naibiidae (Triassic-Eocene);

Dracaphididae (Triassic);

Sinojuraphidiae (Jurassic).



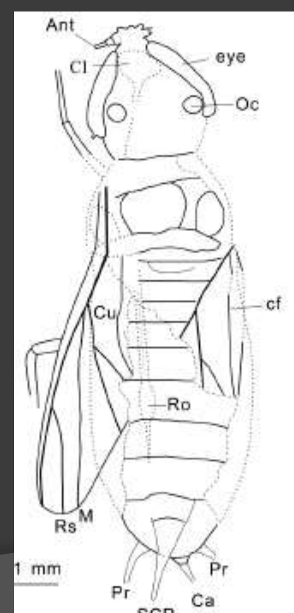
10. *Coccavus supercubitus* Shcherbakov, 2007; Triassic
12. *Panirena sukatshevae* Shcherbakov, 2007; Jurassic

Naibia zherikhini Shcherbakov, 2007; Eocene

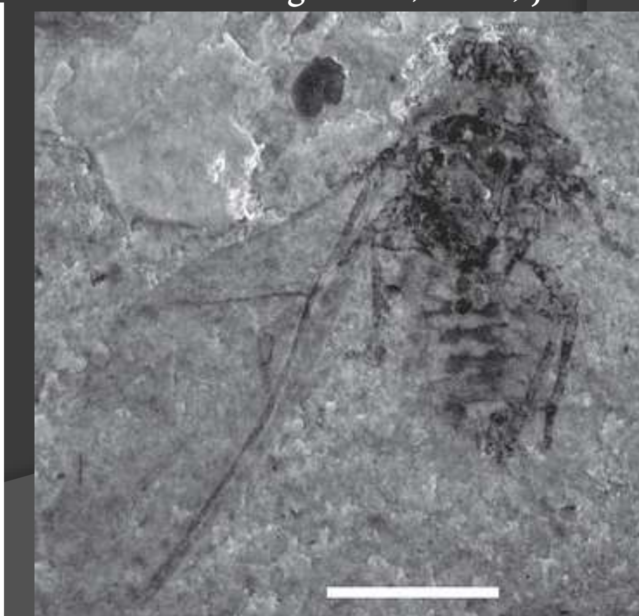
very narrow pterostigma
elongate stem of CuA
Sc fused to radial stem

This group was originally regarded as 'four-winged ancestors of coccids'; but now they are believed to be closely related to aphids because of the body structure.

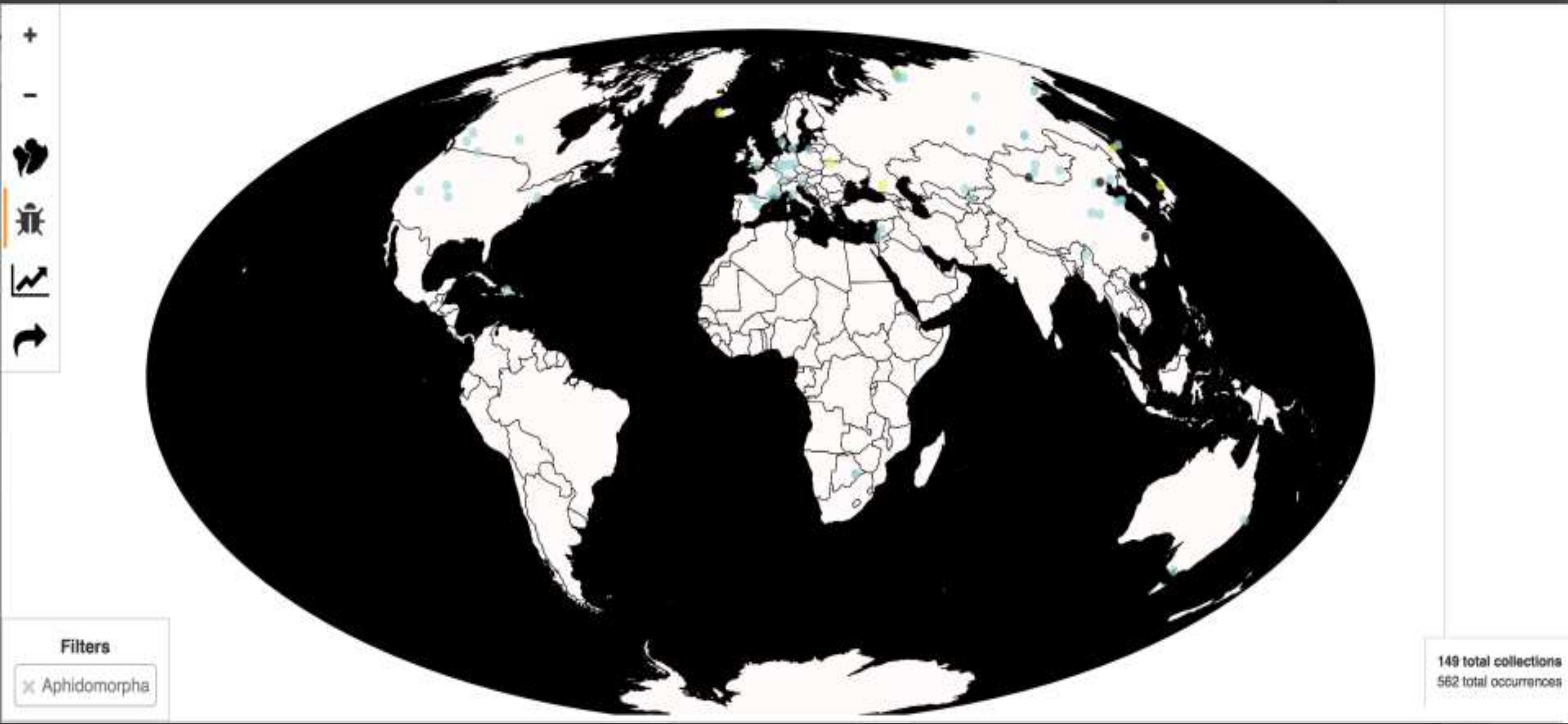
Dracaphis angustata Hong *et al.*, 2009; Triassic



Sinojuraphis ningchengensis Huang et Nel, 2008; Jurassic



Aphidomorpha: aphids, phylloxerans and adeligds



The fossil record of aphids is good, and they are particularly common in deposits from the Cretaceous and Palaeogene, thanks to inclusions in amber. Most abundant findings come from the northern hemisphere, but there are a few from Gondwanaland (southern continents).

Infraordo Aphidomorpha Becker-Migdisova et Aizenberg, 1962

Superfamily Adelgoidea Annand, 1928

- Adelgidae Annand, 1928 – Eocene-Holocene
- Elektraphididae† Steffan, 1968 – Late Cretaceous-Pliocene
- Mesozoicaphididae† Heie in Heie and Pike, 1992 – Late Cretaceous

Superfamily Aphidoidea Latreille, 1802

- Aiceonidae Raychaudhuri, Pal et Ghosh, 1980 – Holocene
- Anoeciidae Tullgren, 1909 – Holocene
- Aphididae Latreille, 1802 – Late Cretaceous-Holocene
- Baltichaitophoridae† Heie, 1980 – Eocene
- Canadaphididae† Richards, 1966 – Cretaceous
- Cretamyzidae† Heie et Pike, 1992 – Late Cretaceous
- Drepanochaitophoridae† Zhang et Hong, 1999– Eocene
- Drepanosiphidae Herrich-Schaeffer in Koch, 1857 – Early Cretaceous-Holocene
- Eriosomatidae Kirkaldy, 1905 – Eocene-Holocene
- Greenideidae Baker, 1920 – Eocene-Holocene
- Hormaphididae Mordvilko, 1908 – Eocene-Holocene
- Lachnidae Herrich-Schaeffer in Koch, 1854 – Miocene-Holocene
- Oviparosiphidae† Shaposhnikov, 1979 – Middle Jurassic-Early Cretaceous
- Parvaverrucosidae† Poinar et Brown, 2005 – Late Cretaceous
- Phloeomyzidae Mordvilko, 1934 – Holocene
- Rasnitsynaphididae† Homan et Wegierek, 2011 – Early Cretaceous
- Sinaphididae† Zhang, Zhang, Hou et Ma, 1989 – Early Cretaceous
- Tamaliidae Oestlund, 1922 – Holocene
- Thelaxidae Baker, 1920 – Early Cretaceous-Holocene

Superfamily Genaphidoidea† Handlirsch, 1907

- Genaphididae† Handlirsch, 1907 – Early Cretaceous

Superfamily Palaeoaphidoidea† Heie, 1981

- Juraphididae† Żyła, Blagoderov et Wegierek, 2014 – Middle Jurassic-Early Cretaceous
- Palaeoaphididae† Richards, 1966 – Cretaceous
- Shaposhnikoviidae† Kononova, 1976 – Late Cretaceous
- Szelegiewicziidae† Wegierek, 1989 – Middle Jurassic-Early Cretaceous

Superfamily Phylloxeroidea Steffan, 1968

- Phylloxeridae Herrich-Schäffer in Koch, 1857 – Eocene-Holocene

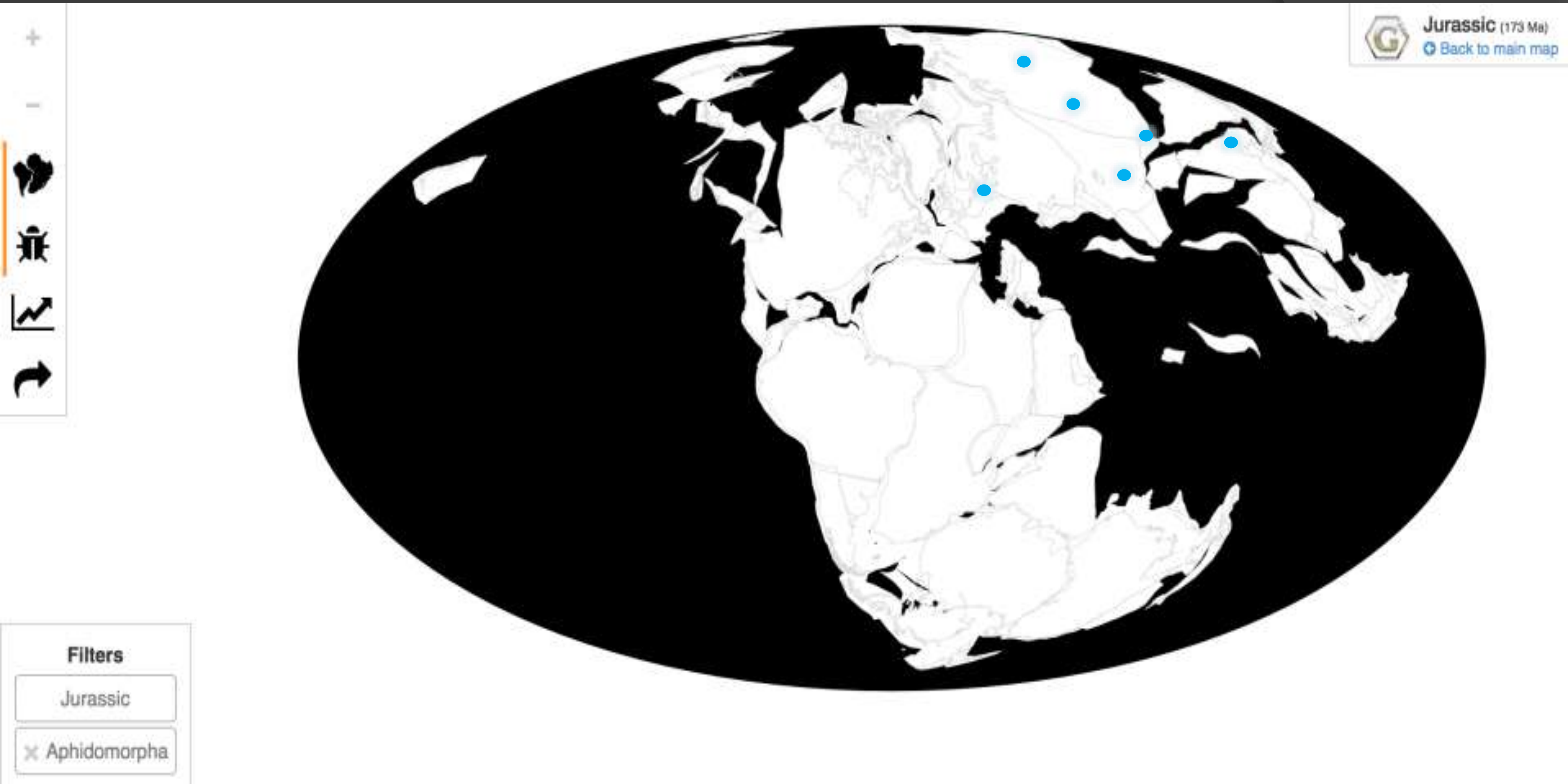
Superfamily Tajmyraphidoidea† Kononova, 1975

- Burmaphididae† Poinar et Brown, 2005 – Cretaceous
- Grassyaphididae† Heie in Heie et Azar, 2000 – Late Cretaceous
- Khatangaphididae† Heie in Heie et Azar, 2000 – Late Cretaceous
- Lebanaphididae† Heie in Heie et Azar, 2000 – Early Cretaceous
- Retinaphididae† Heie in Heie et Azar, 2000 – Late Cretaceous
- Tajmyraphididae† Kononova, 1975 – Late Cretaceous

Superfamily Triassoaphidoidea† Heie, 1991

- Creaphididae† Shcherbakov et Wegierek, 1991 – Middle Triassic
- Triassoaphididae† Heie, 1991 – Middle Triassic
- Leaphididae† Shcherbakov, 2010 – Middle Triassic
- Lutevanaphididae† Szwedo, Lapeyrie et Nel, 2015 – Early Permian

The taxonomic diversity of fossil aphids is very high, with 4 extinct superfamilies

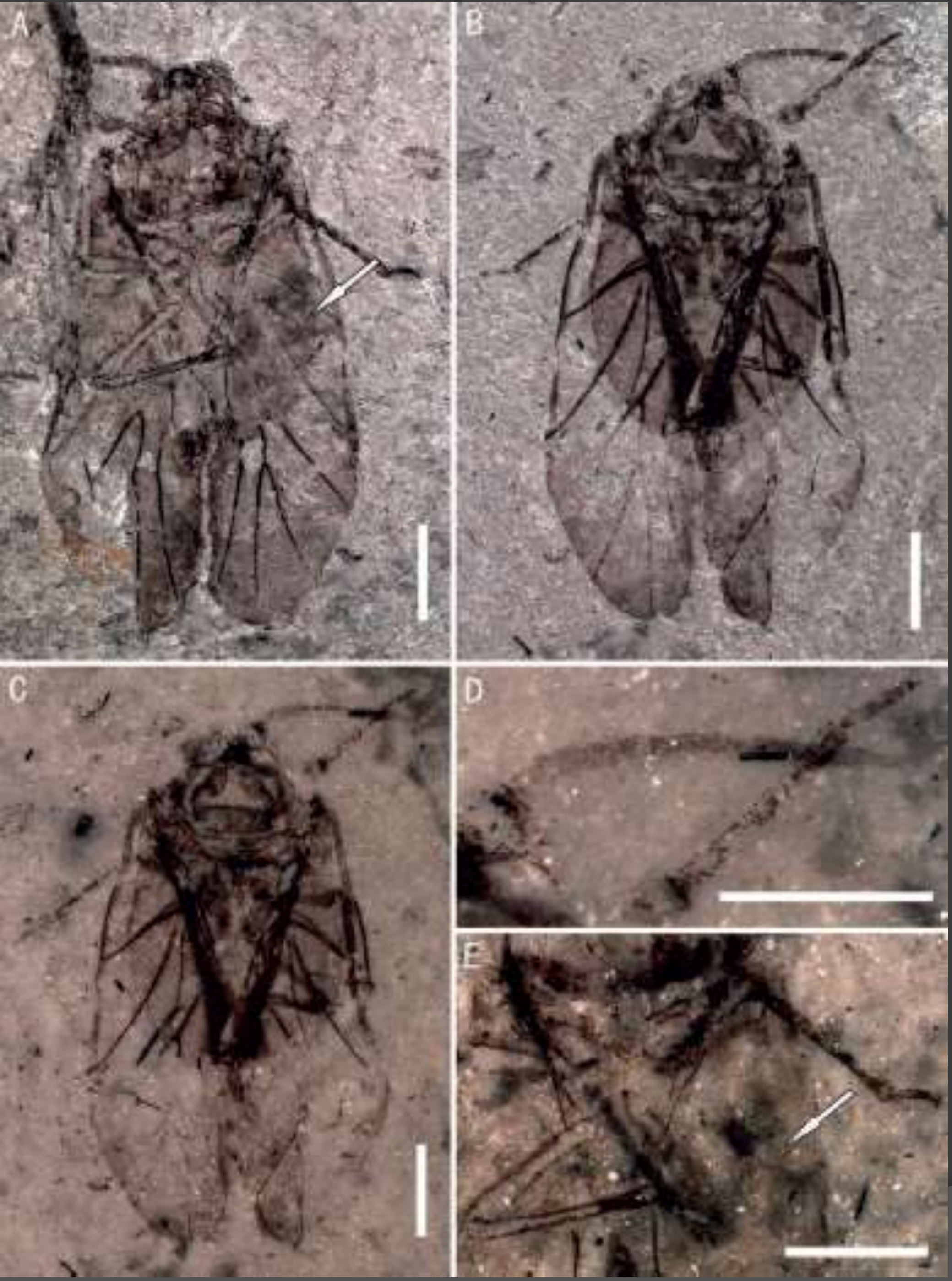


Jurassic aphids are only known from Eurasia, with some records belonging to three extinct families:

Juraphididae

Szelegiewicziidae (Palaeoaphidoidea)

Oviparosiphidae (Aphidoidea)

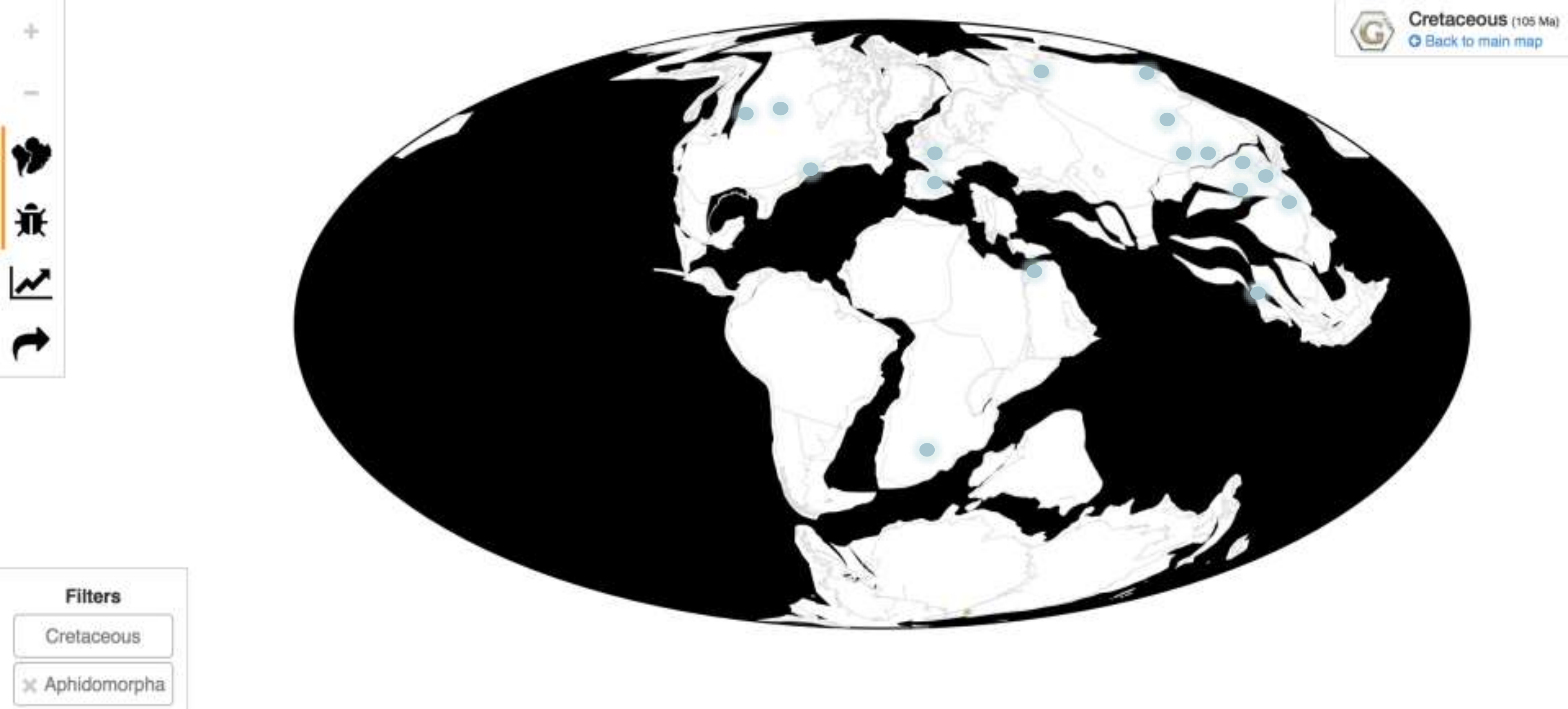


Jurassic aphids (160 mya)

forewings similar in structure to the modern aphids;
hindwings strongly reduced, with venation simplified;
antennae 7-segmented;
secondary rhinaria grouped in rows;
terminal spine developed;
compound eyes well developed;
Ovipositor and cauda.

These Jurassic aphids probably had a simple life cycle.

Oviparosiphidae
Daoaphis magnalata Huang *et al.*, 2015



Cretaceous families:

Elektraphididae
Aphididae
Canadaphididae
Cretamyzidae
Drepanosiphidae
Oviparosiphidae
Parvaverrucosidae

Rasnitsynaphididae
Sinaphididae
Thelaxidae
Genaphididae
Juraphididae
Palaeoaphididae
Shaposhnikoviidae
Szelegiewicziidae

Burmaphididae
Grassyaphididae
Khatangaphididae
Lebanaphididae
Retinaphididae
Tajmyraphididae

The highest diversity at family level of aphids dates from the Cretaceous (145-66 mya), with some families restricted to this period. There are much more undescribed aphids from the Cretaceous, both from sedimentary deposits and inclusions in amber.

Genaphididae

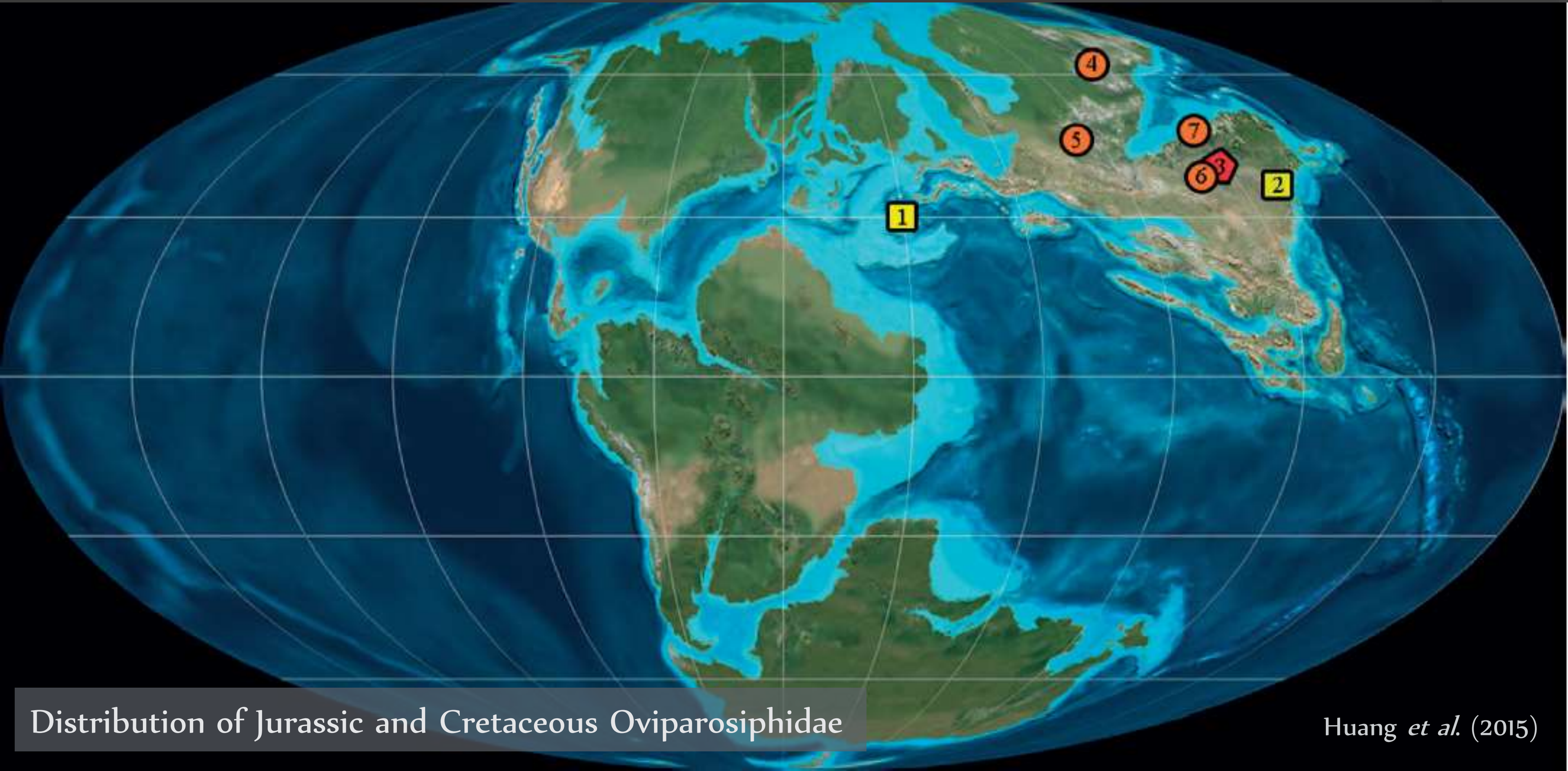
Szelegiewicziidae

Thelaxidae

Oviparosiphidae

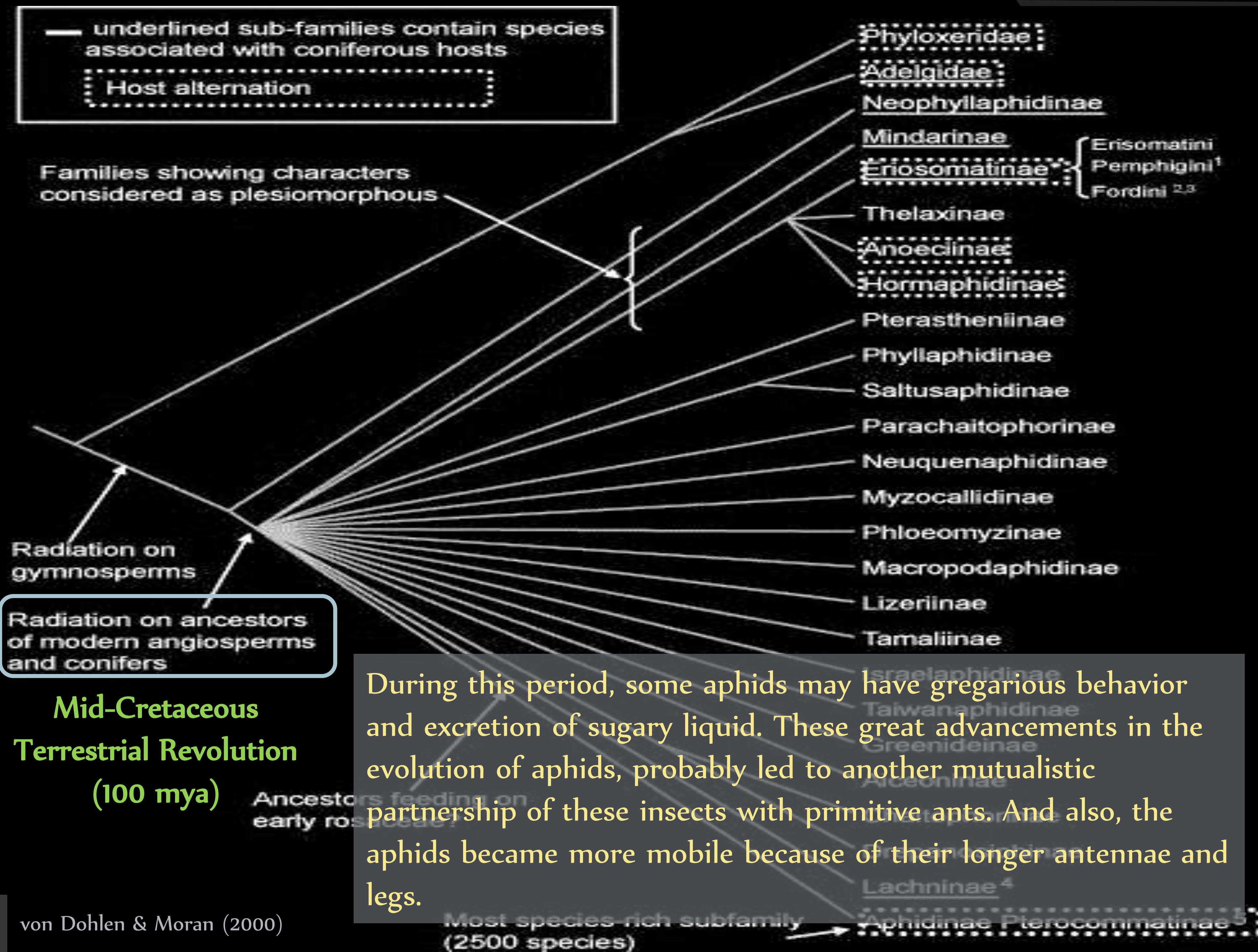
New family? from Burmese amber

- Extant aphid families had already appeared during the Cretaceous but were rare, whereas most Mesozoic aphids belong to extinct families.
- Aphids are rare in tropical regions (such as Burmese amber), but are common in temperature area, like the distribution of extant aphids.



Distribution of Jurassic and Cretaceous Oviparosiphidae

Huang *et al.* (2015)



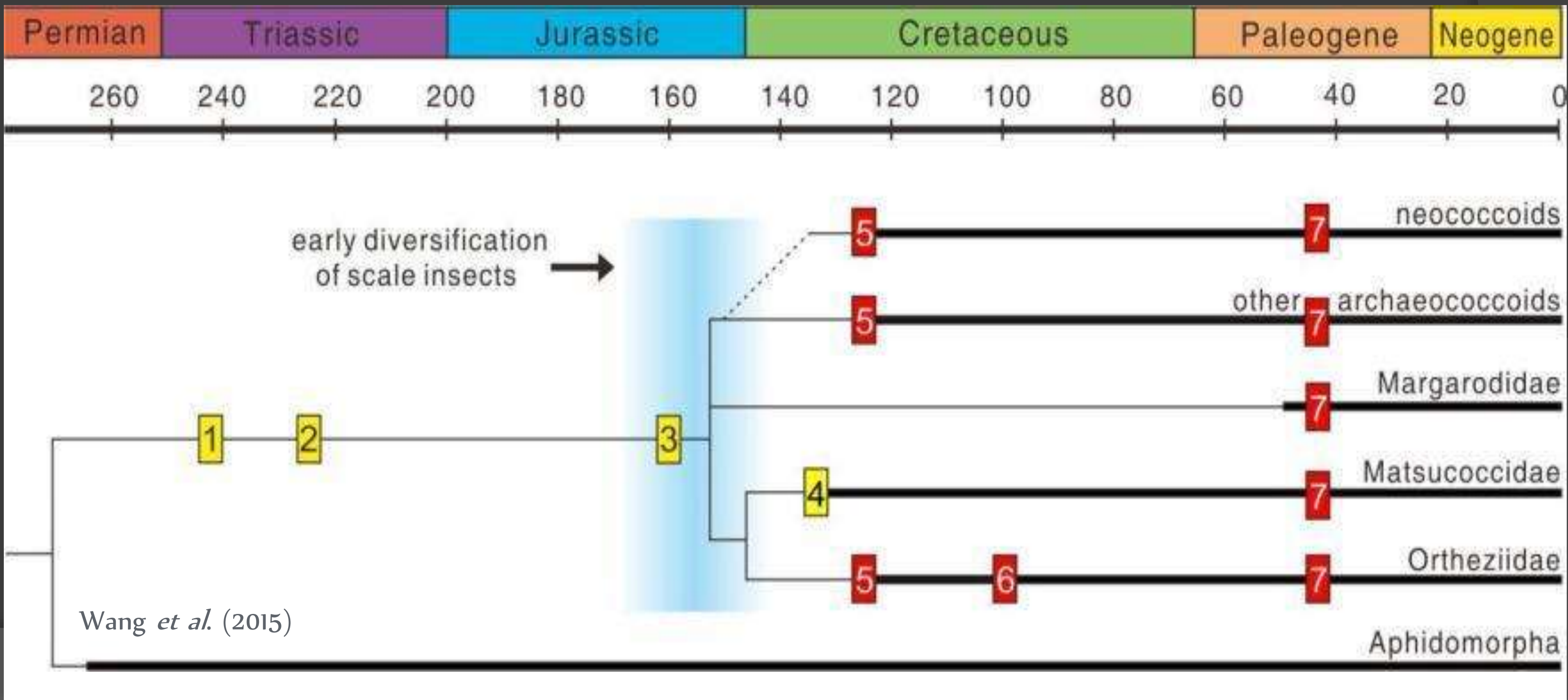
Mid-Cretaceous Terrestrial Revolution (100 mya)

During this period, some aphids may have gregarious behavior and excretion of sugary liquid. These great advancements in the evolution of aphids, probably led to another mutualistic partnership of these insects with primitive ants. And also, the aphids became more mobile because of their longer antennae and legs.

von Dohlen & Moran (2000)

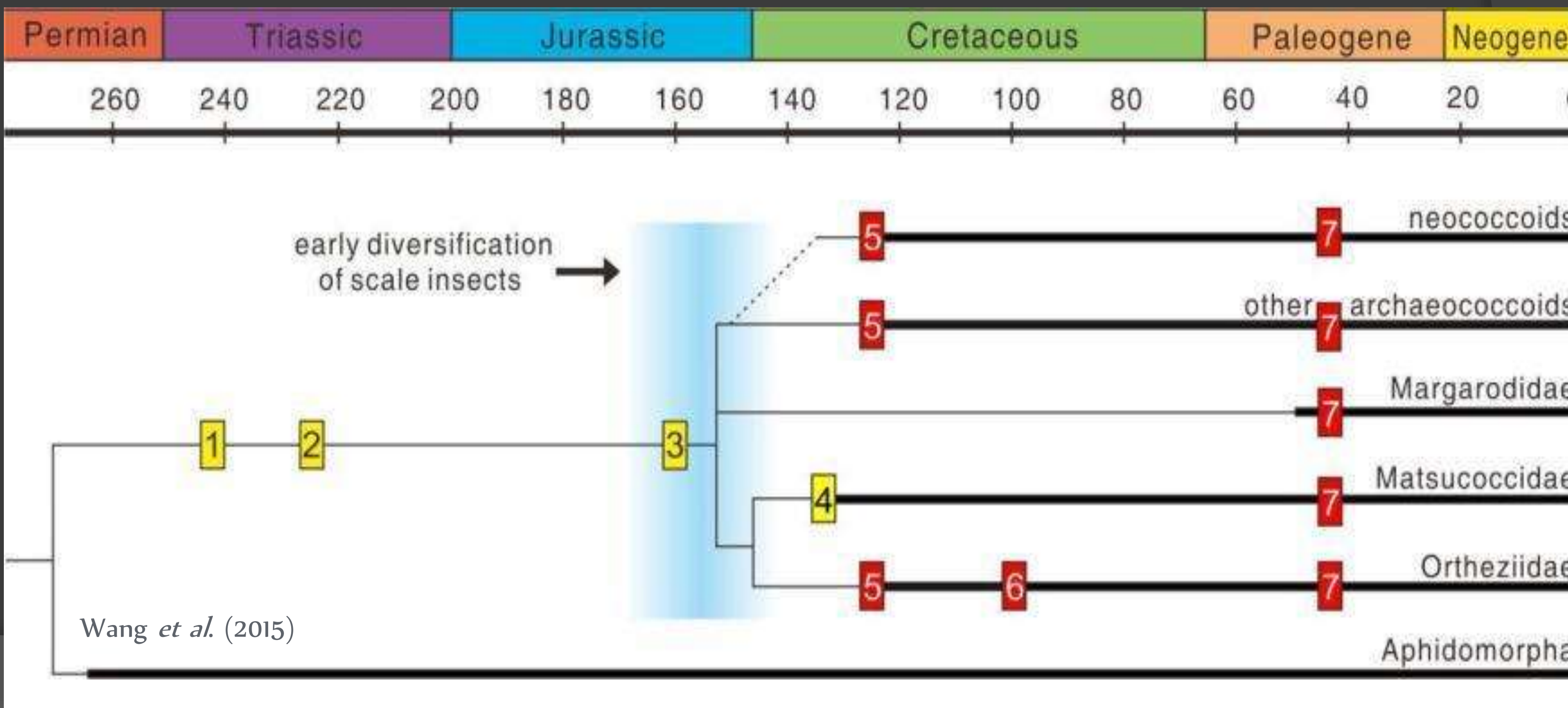
The early evolution of scale insects

- The early evolution of scale insects is still a mystery. Probably they split from common ancestor with aphids somewhere in the Permian.
- Probably ancestral coccids lived in litter or soil, feeding on roots, and this condition among recent taxa seems to be very ancient.
- We do not have any direct record until the Early Cretaceous, when they appear as highly diversified group with number of families of archaeococcids.

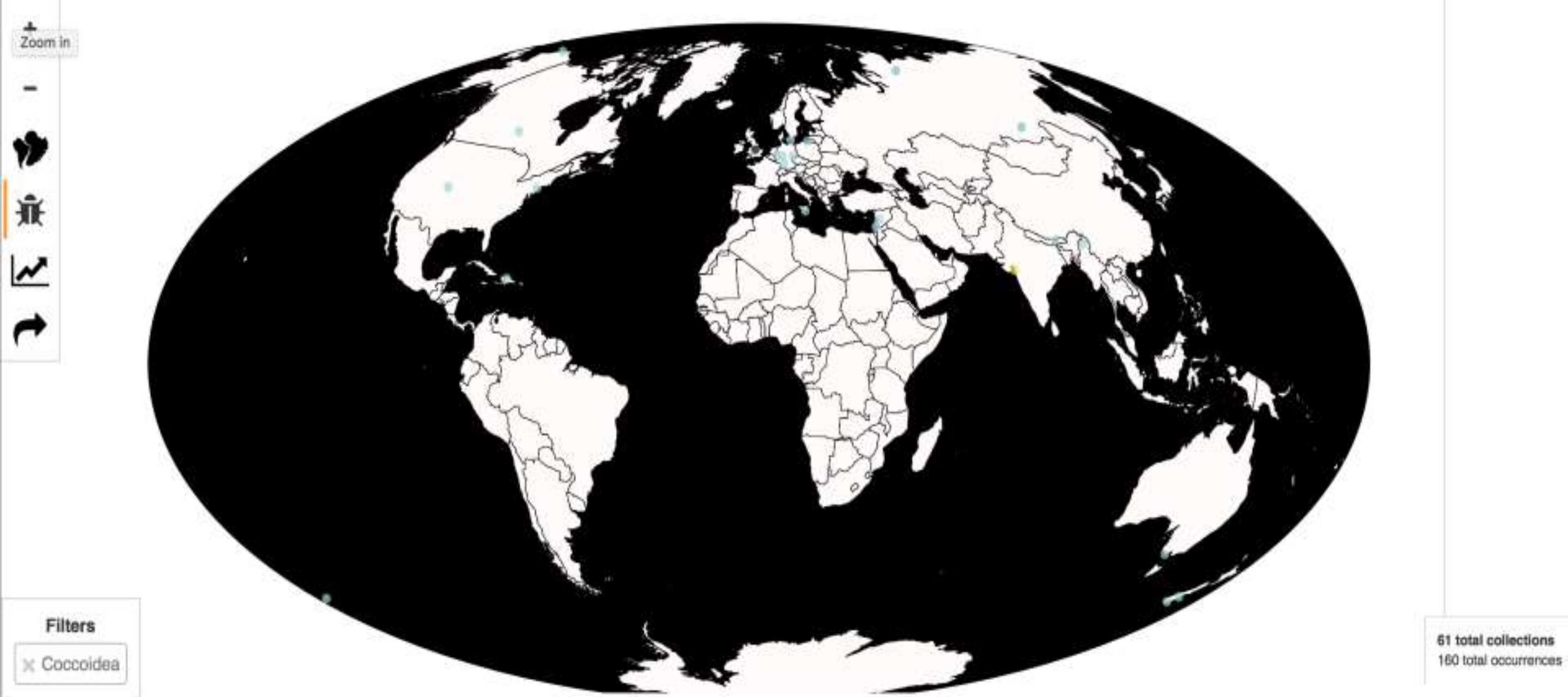


A simplified history of scale insects

(1) There are undescribed scale marks on plants from the Middle Triassic of Italy; (2) Also, scale marks on plants from the Late Triassic of South Africa; (3) undescribed scale insects from the Late Jurassic; Fossil evidence show an early diversification of scale insects probably occurred during the end of the Jurassic or earliest Cretaceous (blue area), and later radiations are probably closely related to the rise of angiosperms and ants.



Wang *et al.* (2015)

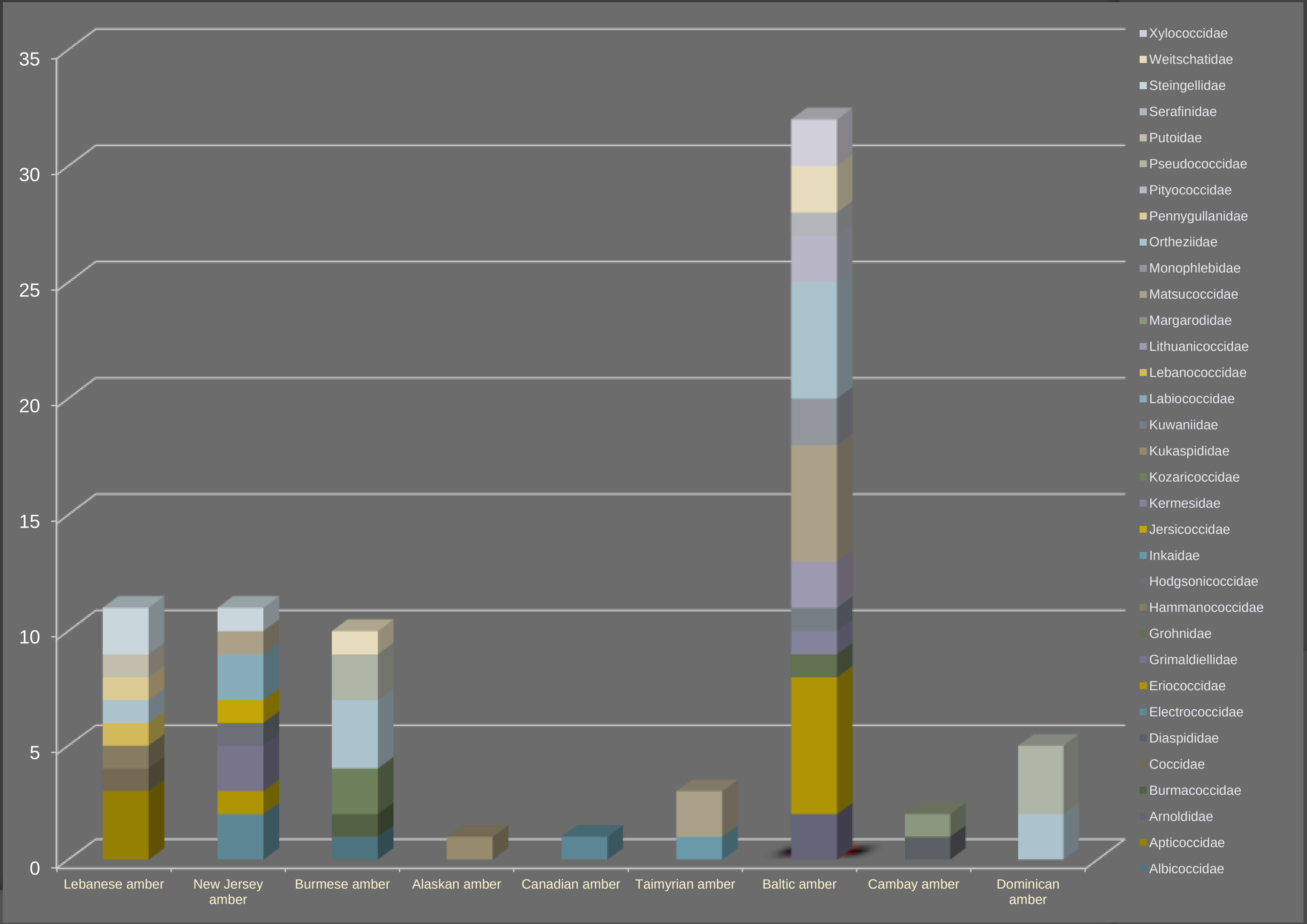


Extinct families:

Apticoccidae
Arnoldidae
Burmacoccidae
Electrococcidae
Grimaldiellidae
Groehnidae
Hammanococcidae
Jersicoccidae
Kozariidae
Kukaspididae
Labiococcidae
Lebanococcidae
Lithuanicoccidae
Pennygullaniidae
Serafinidae
Weitschatidae
Albicoccidae
Hodgsonicoccidae
Inkaidae

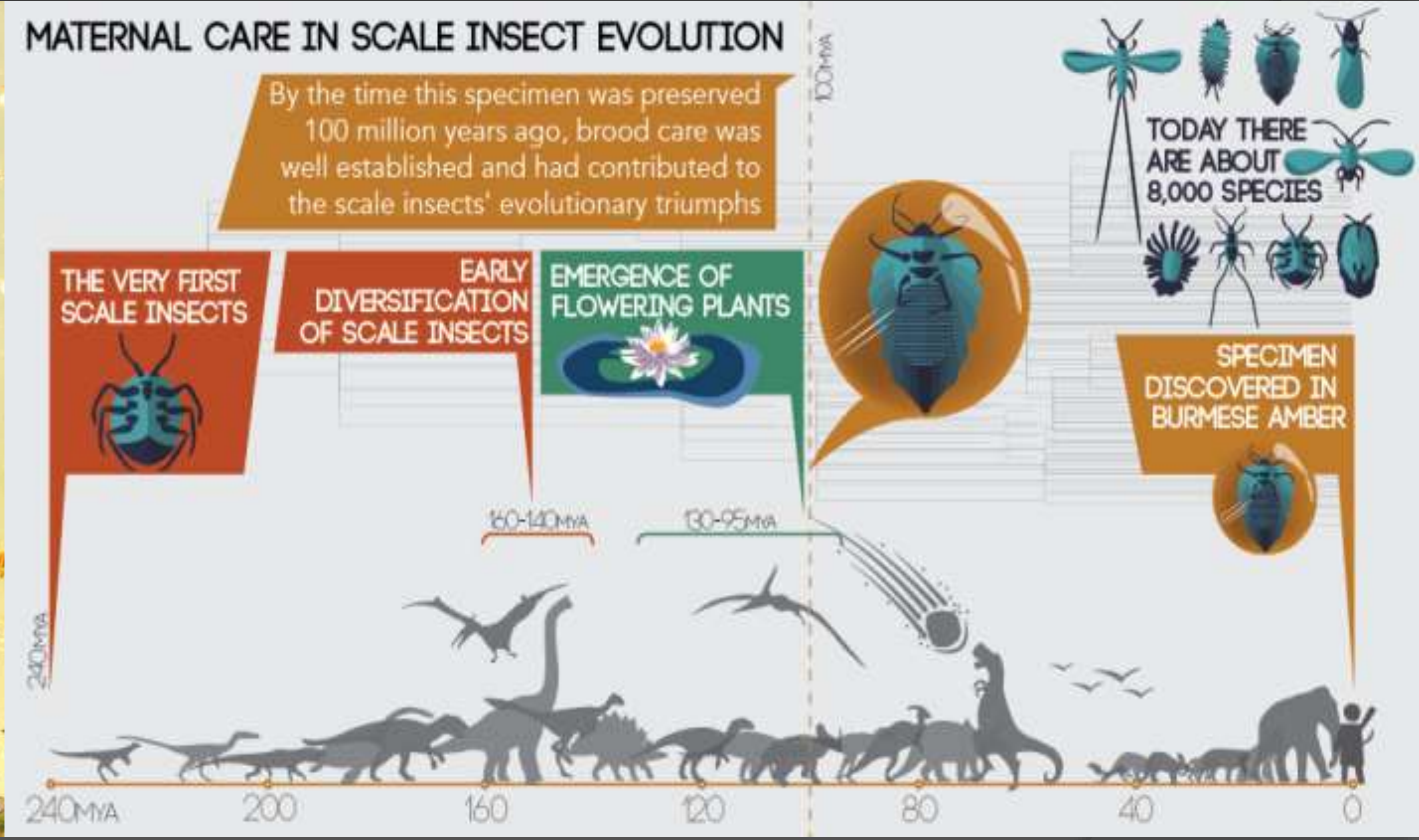
The fossil record of scale insects is relatively rich, but mainly the fossils preserved in amber have been studied. There are some new findings of extinct scale insects from the Early Eocene Indian amber (50 mya) and the Miocene of Chinese Zhangpu amber (15 mya).

Scale insect families in various fossil ambers – 33 families recorded in total



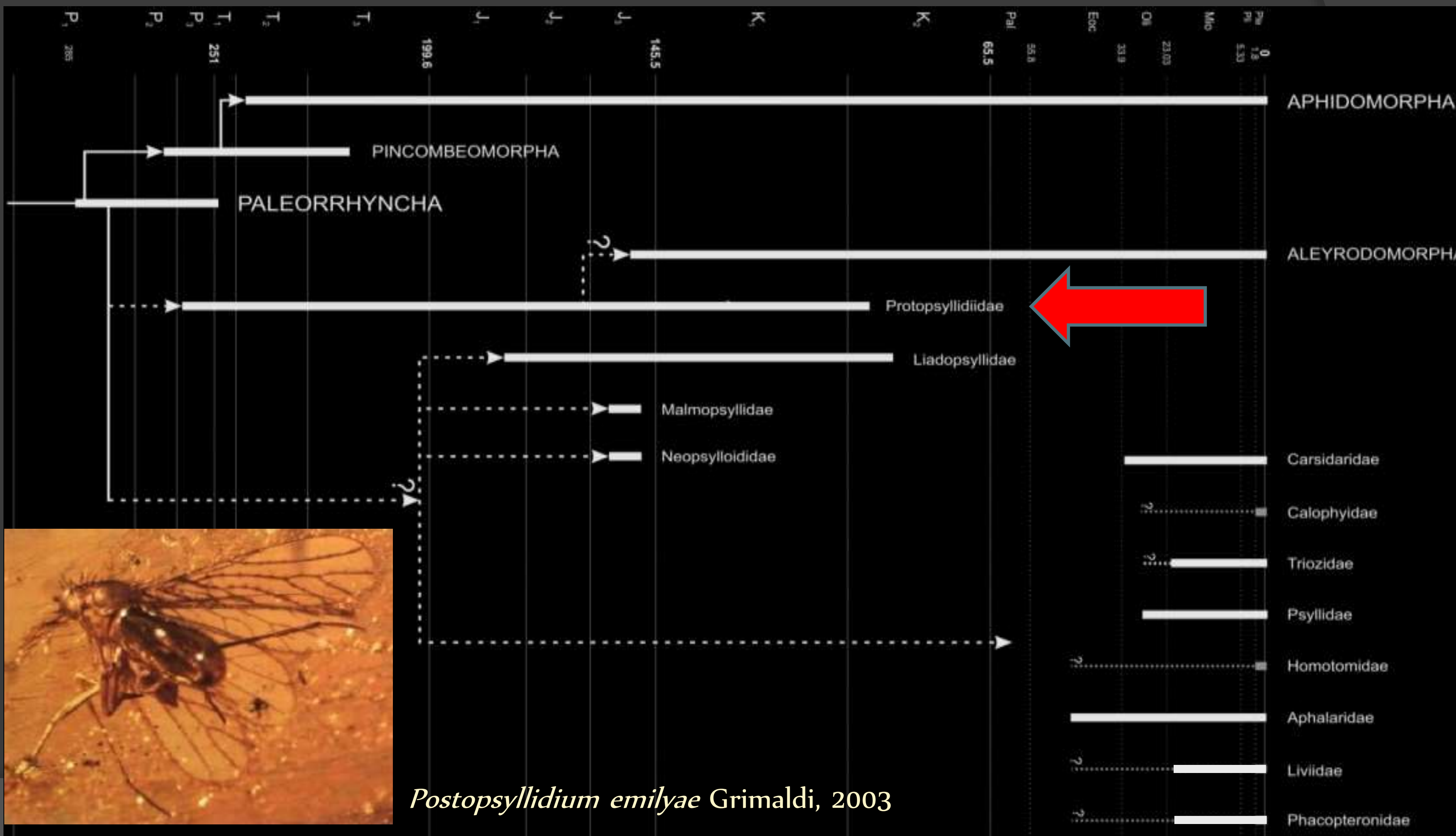
- In 2015, we reported an ensign scale insect (Hemiptera: Ortheziidae) from mid-Cretaceous Burmese amber. It has eggs within a wax ovisac, and several freshly hatched nymphs.
- This fossil represents the earliest direct evidence of brood care in the insect fossil record.
- Brood care could therefore have been an important driver for the early radiation of scale insects.

Wang *et al.* (2015)



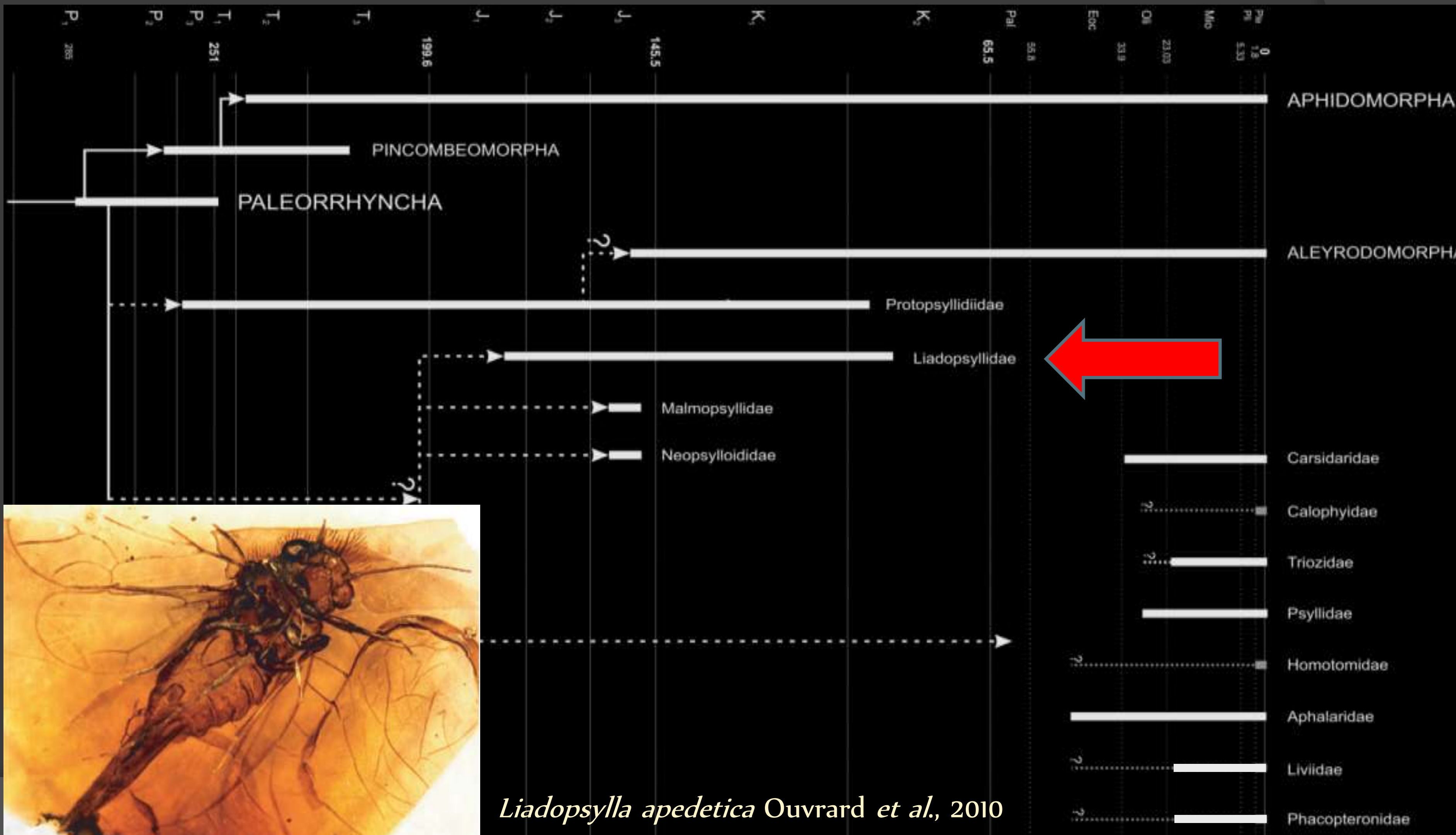
The early evolution of psyllids (Psylloidea)

The third branch of sternorrhynchan includes Psylloidea and Aleyrodoidea. The oldest representatives (Protopsyllidiidae) are quite abundant as fossils from the Permian to Early Cretaceous (270–100 mya).



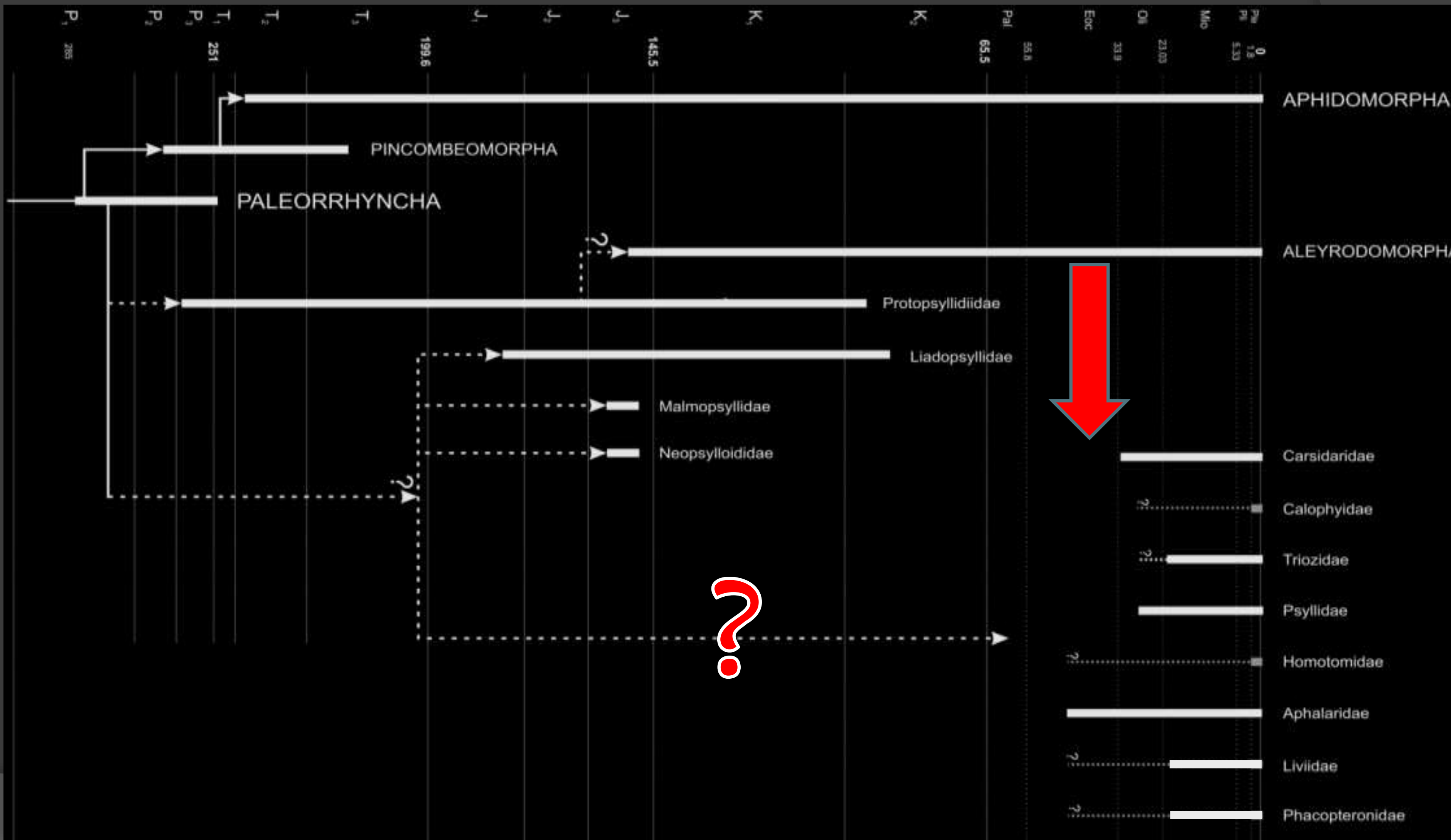
Postopsyllidium emilyae Grimaldi, 2003

Three extinct families were known from the Jurassic. Among them, the family Liadopsyllidae is widespread in Early Cretaceous amber. These extinct psyllids probably cannot jump.



Liadopsylla apedetica Ouvrard *et al.*, 2010

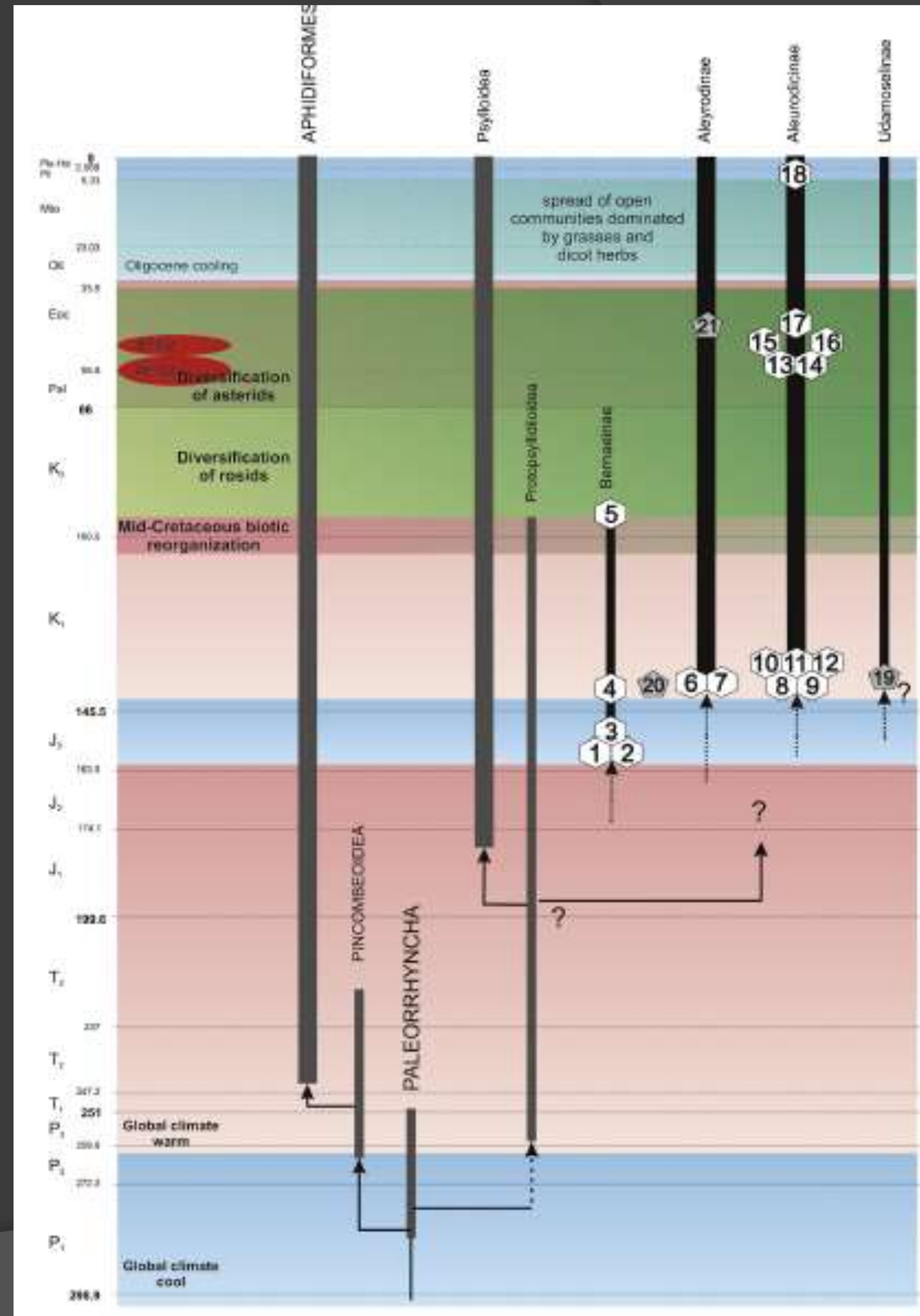
Two modern families appear in the Eocene (50 mya); and other extant families are reported from the Miocene (20 mya). Why psyllids are not common among fossils - this question remains open.



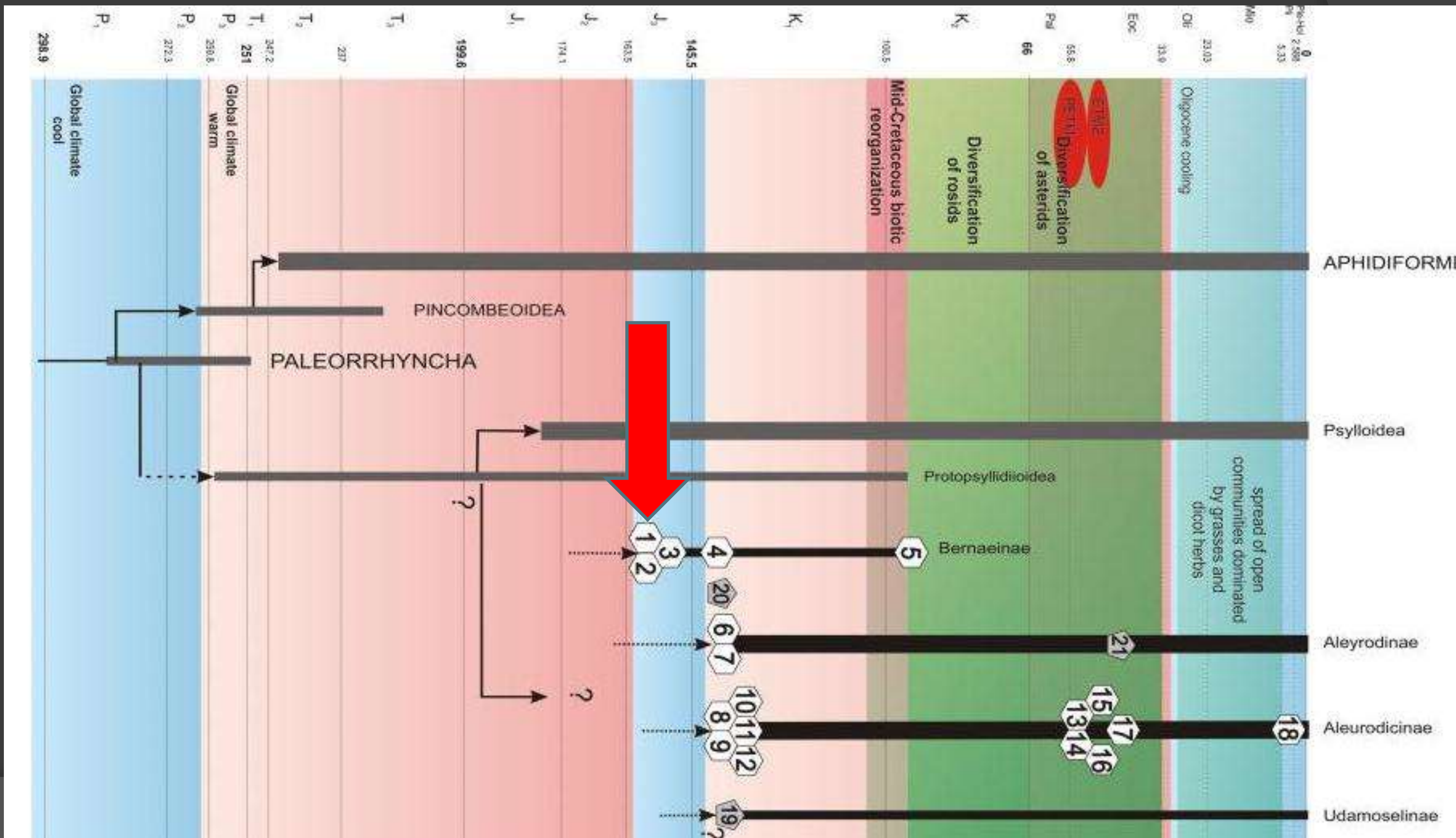
The early evolution of whiteflies (Aleyrodoidea)

Aleyrodoidea

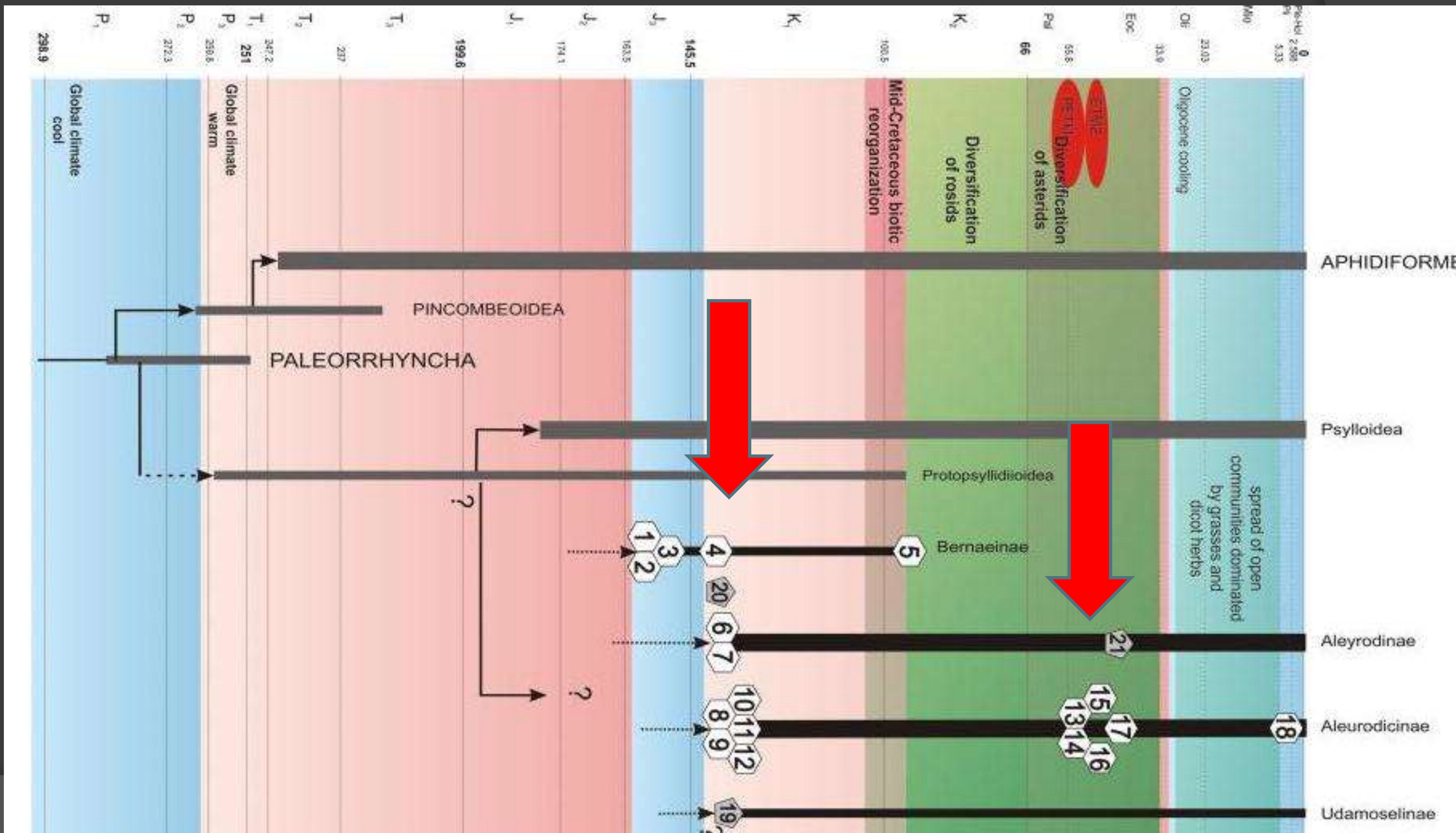
- the oldest known fossils from the Mid-Late Jurassic (160 mya);
- decreasing number of antennal segments;
- tendency to separate the compound eye into two portions;
- miniaturization;
- reduction of venation of both wings;
- reduction of clavus;
- loss of M and claval veins
- hind legs jumping
- imagines and nymphs covered with wax and wax-derived substances;
- four instars feeding, fifth instar non-feeding;
- fifth instar – resting stage (pupa)



The oldest whiteflies come from the Late Jurassic of Daohugou (undescribed) and Karatau (160 mya). They belong to the extinct subfamily Bernaeinae. In the Early Cretaceous, this group is still present, but extant subfamilies appeared.

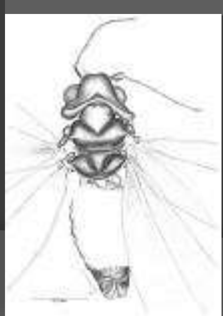
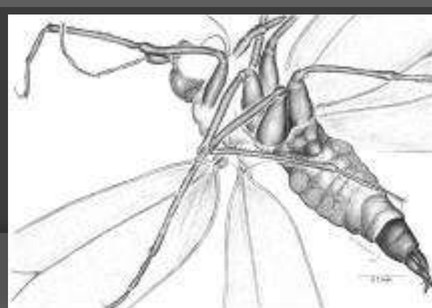


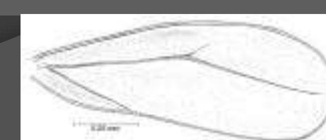
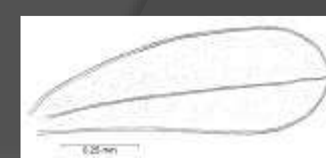
Three subfamilies were recorded from the Early Cretaceous ambers. Diverse whiteflies are preserved in early Eocene Oise amber, more specimens come from Baltic amber. All these are imagines. The only described puparium comes from the Pliocene of Germany.



Szwedo & Drohojowska (2016)

Also among fossil whiteflies the spectacular fossils could be found. This piece of Baltic amber contains 12 specimens of whiteflies, belonging to the subfamily Aleyrodinae. It is the first record of gregarious behavior of whiteflies.

Conclusion

- Sternorrhynchan insects are rarely fossilized because they have small and delicate bodies.
- The oldest Sternorrhyncha are traced back to the Permian, but they may have originated in the Carboniferous (300 mya).
- Aphids are traced back to the Permian, with several records from the Triassic. They underwent a rapid radiation into the current tribes after shifting from gymnosperms to angiosperms some time during the Late Cretaceous.

- The oldest fossil scale insects are from the Early Cretaceous. The oldest scale marks on plants are from the Triassic but scales probably really of Permian age. The earliest radiation of the neococcoids is probably in conjunction with the rise of Cretaceous flowering plants.
- Protopsyllidiidae are reported from the Late Permian to Cretaceous. Modern psyllid families appear in the Eocene, but they probably diversified in the Cretaceous.
- Whiteflies extend back into the Jurassic (160 mya), and they may have originated in the Late Permian or even earlier. Modern subfamilies probably appeared during the Cretaceous.

- The fossil record of Sternorrhyncha is very complicated, with numerous gaps, and sudden appearances of highly diverse and specialized groups.
- The evolutionary history of Sternorrhyncha was shaped by global geological and biological events, such as massive extinctions and biotic changes.
- There are many fossils still waiting to be studied. New fossils will be described in the near future, and may provide a good opportunity to test the hypotheses based on molecular investigations.

THANKS FOR YOUR ATTENTION!

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The fossil record of Sternorrhyncha

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