Fossil records and evolution of haematophagy in biting midges (Diptera: Ceratopogonidae)

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Biting midges is a family of small (1-6 mm) nematocerous flies

Ceratopogonids have nearly global distribution and are known to occur in various habitats ranged from coastal areas to high mountains (up to 4 000 m.a.s.l).

Immatures are found in all types of aquatic, semiaquatic and true terrestrial habitats. Larvae are herbivorous, fungivorous, saprophagous, or carnivorous.

Adult males feed exclusively on nectar.
Females of most genera need protein-rich meal and are predators or ectoparasites (invertebrate haemolymph & vertebrate blood).

Extant Ceratopogonidae are included into 4 subfamilies, 111 genera and 6 267 species

Among them, members of 3 subfamilies represented by 3 genera and 1 subgenus are thought to be haematophagous:

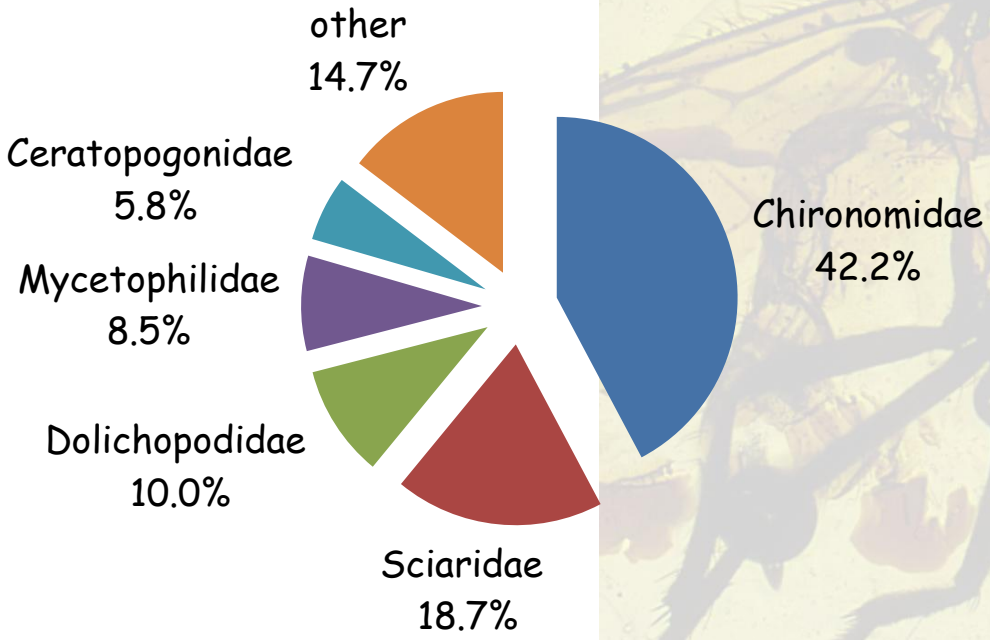
- *Austroconops* (2 spp.),
- *Leptoconops* (150 spp.),
- *Culicoides* (1 368 spp.),
- subgenus *Lasiohelea* of *Forcipomyia* (184 spp.).

Bloodsucking ceratopogonids are annoying biters of humans and of wild and domestic animals

They can act as vectors of:

- 66 viruses (i.a. bluetongue and Akabane viruses),
- 15 species of protozoan parasites (e.g. those causing avian malaria and leishmaniasis),
- 26 species of filarial nematodes (e.g. *Onchocerca* sp., *Icosiella neglecta*).

Biting midges are well documented as fossils, and their inclusions are common in ambers, e.g. in Baltic amber they represent 5.8% of dipterans



The oldest one, *Archiaustroconops besti* Borkent, Coram et Jarzembowski, 2013, is dated to 142 Ma (Lower Cretaceous) and was described from female wing from limnestone formations of Dorset, UK.

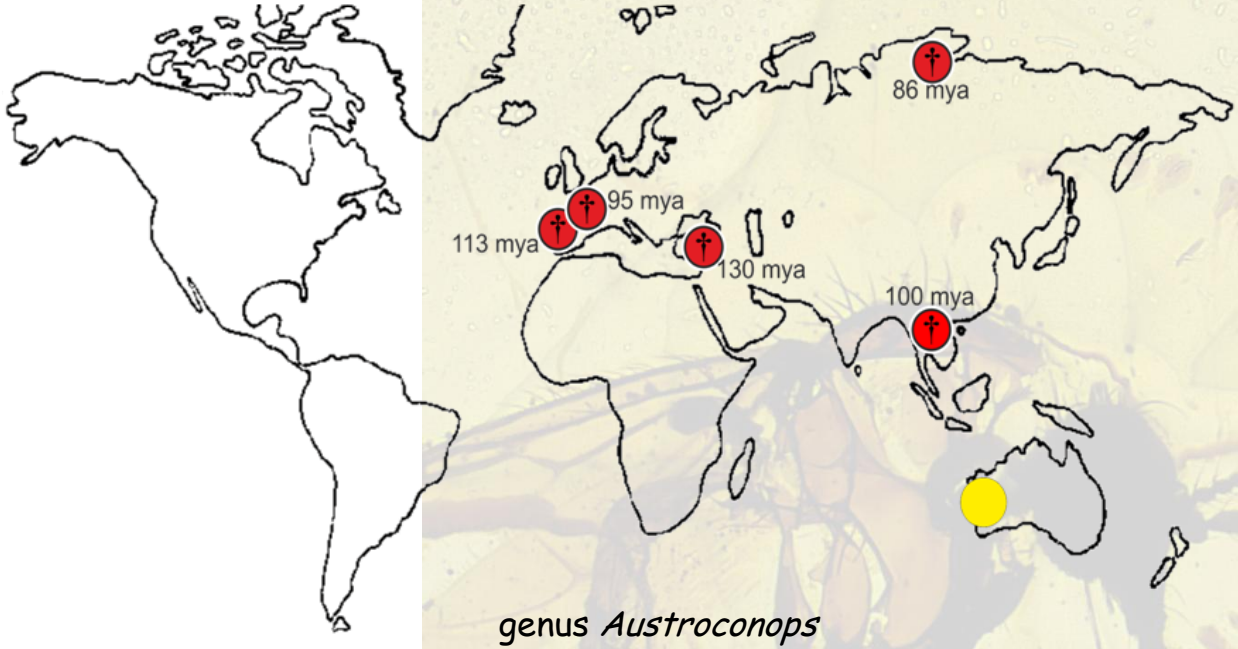
Fossil records of biting midges

- Purbeck Limestone Group of Dorset, United Kingdom (Lower Cretaceous, 142 Ma). 1 genus, 1 species.
- Lebanese amber (Lower Cretaceous, 130 Ma). 8 genera, 31 species.
- Austrian amber (Lower Cretaceous, 129 Ma). 1 genus, 1 species.
- Spanish amber (Lower Cretaceous, 113-101 Ma). 5 genera, 8 species.
- Burmese amber (Upper Cretaceous, 100 Ma). 5 genera, 12 species.
- French (NW) amber of Anjou (Upper Cretaceous, 95 Ma). 2 genera, 3 species.
- French (NW) amber of Vendée (Upper Cretaceous, 95-85 Ma). 2 genera, 2 species.
- French (SW) amber of Charentes (Upper Cretaceous, 95 Ma). 1 genus, 1 species.
- French (SE) amber of Provence (Upper Cretaceous, 85 Ma). 2 genera, 2 species.
- New Jersey amber (Upper Cretaceous, 93 Ma). 7 genera, 14 species.
- Siberian amber (Upper Cretaceous, 86 Ma). 7 genera, 16 species.
- Hungarian amber (Upper Cretaceous, 84 Ma). 2 genera, 2 species.
- Canadian amber (Upper Cretaceous, 78 Ma). 9 genera, 19 species.
- Fushun amber (Eocene, 53 Ma). 4 genera, 5 species.
- Sakhalin amber (Eocene, 45 Ma). 4 genera, 2 species.
- Baltic amber (including Danish, Lithuanian, Scandinavian, Saxonian, Ukrainian, Sambian or amber from Bitterfeld, Rovno, Bay of Gdańsk, Sambia, Poland, Russia, etc.) (Eocene, 45 Ma). 26 genera, 109 species.

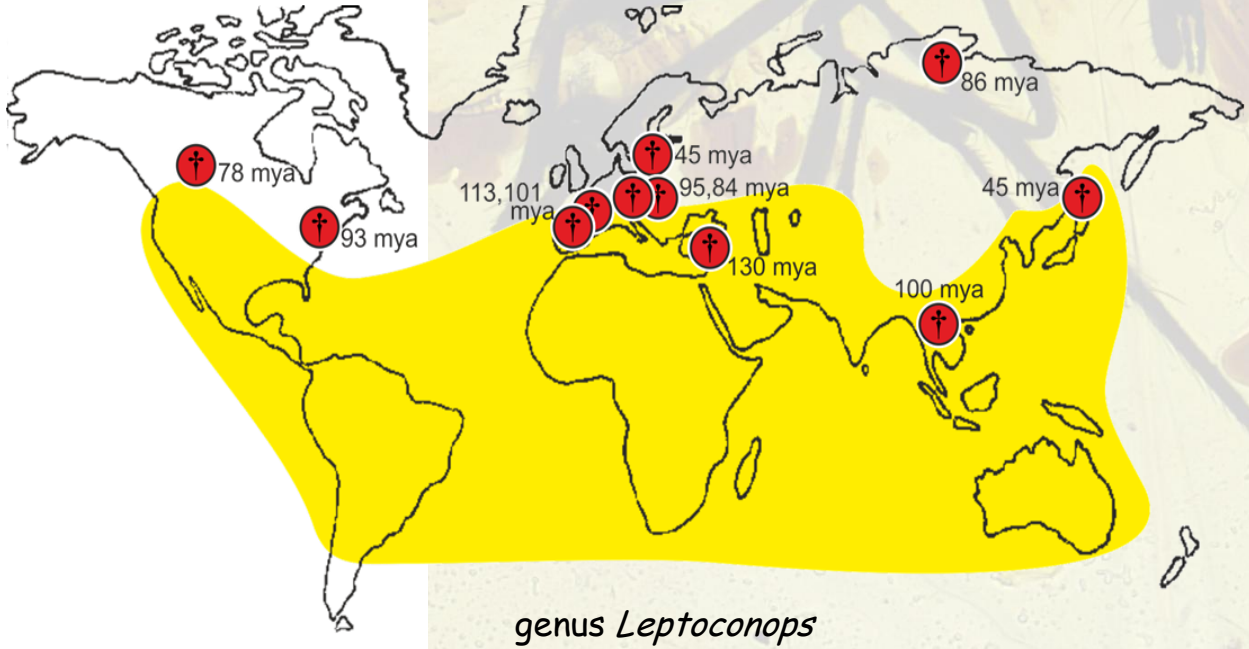
- Bembridge Marls, Isle of Wight, United Kingdom (Oligocene, 35 Ma). 3 extant genera, 1 species.
- Rott Formation, Germany (Miocene, 23-20 Ma). 5 extant genera, 16 species.
- Calico Mts., Mojave Desert, California, USA (Miocene, 20 Ma). 3 extant genera, 17 species (including 2 spp. unplaced).
- Dominican amber (Miocene, 20 Ma). 11 extant genera, 29 species.
- Mexican amber (Miocene, 20 Ma). 5 extant genera.

In total, over 280 fossil species of biting midges belonging to 48 genera (25 extant, 23 extinct) have been described

112 of these species – from the subfamilies Lebanoculicoidinae (4 spp.) and Leptoconopinae (50 spp.), the genera *Archiculicoides* (8 spp.) and *Culicoides* (47 spp.), and the subgenus *Lasiohelea* of *Forcipomyia* (3 spp.) – fed on vertebrate blood.



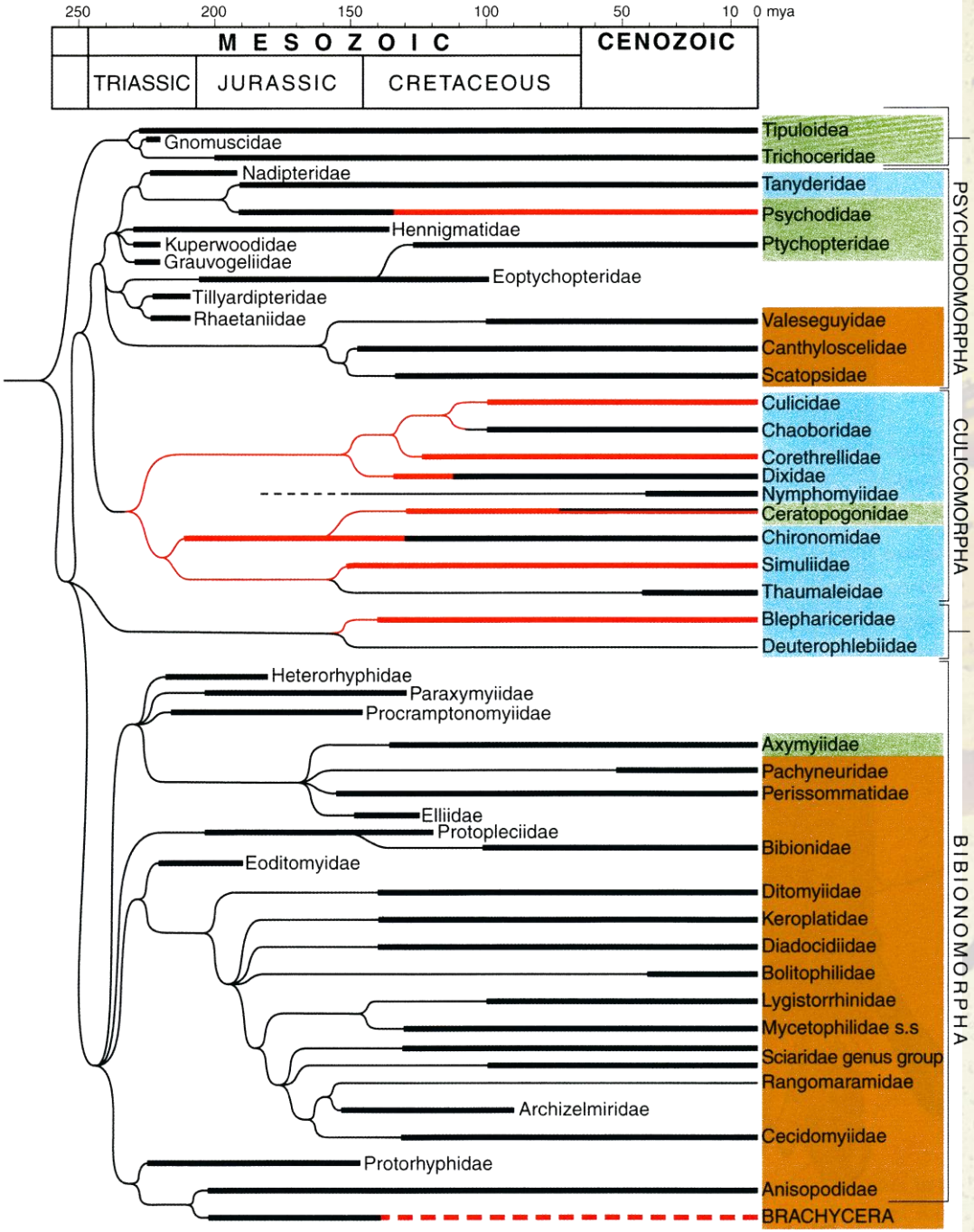
genus *Austroconops*



genus *Leptoconops*

Phylogeny of the basal (nematocerous) Diptera, indicating larval habitats and lineages with blood-feeding adults

Thick lines indicate the extenct of the known fossil record for that lineage.

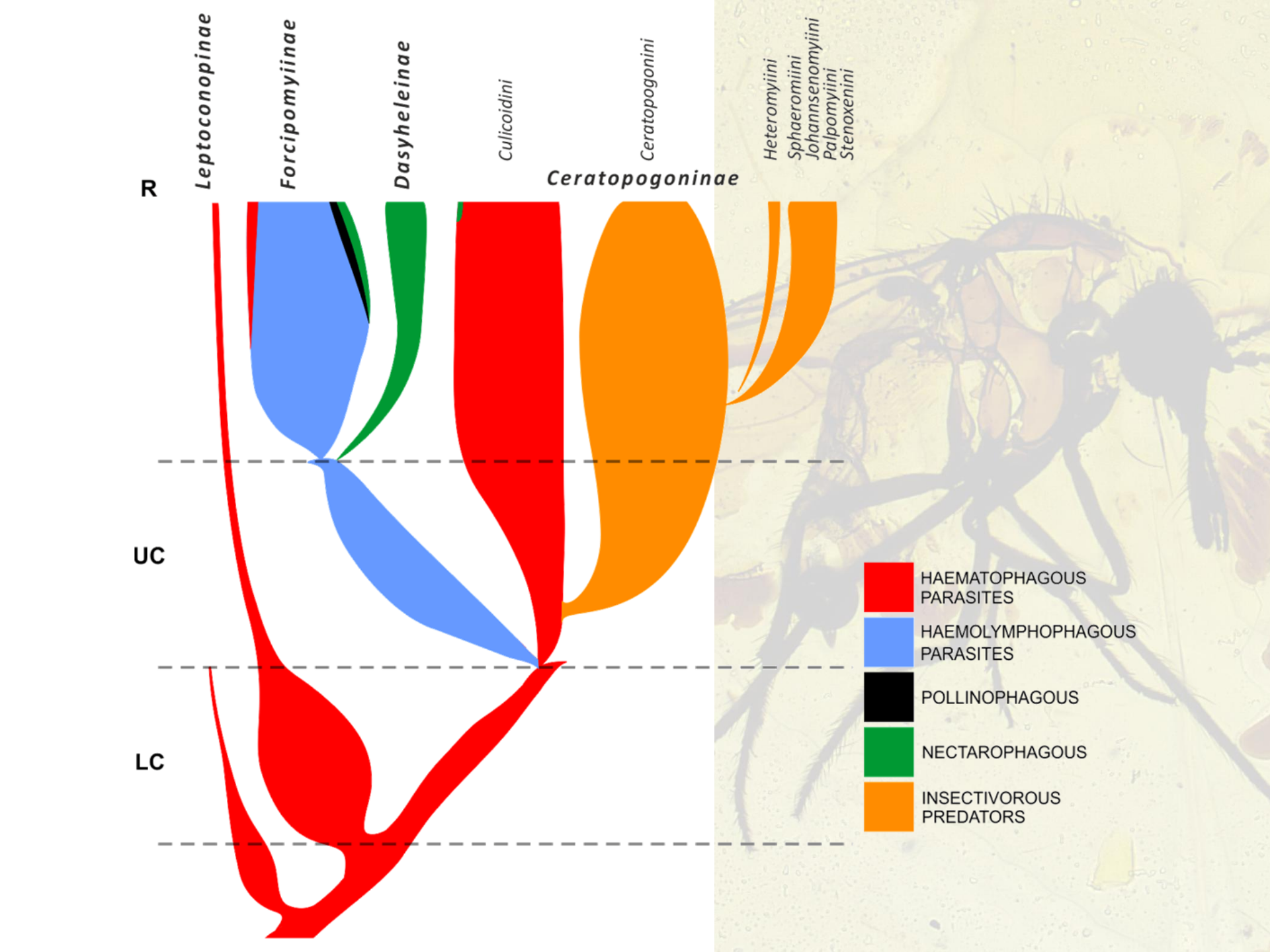


Larval Habitats

- Most are fully aquatic
- Most are semi-aquatic / in wet soils
- Terrestrial (in fungi, humus, rotten wood,…)

- Adult diet of vertebrate blood or insect hemolymph

*after Grimaldi D. & Engel M.S. 2005. Evolution of Insect. Cambridge University Press, 755 pp, changed.


Leptoconopinae
Forcipomyiinae
Dasyheleinae
Culicoidini
Ceratopogonini
Ceratopogoninae
Heteromyiini
Sphaeromiini
Johannsenomyiini
Palpomyiini
Stenoxenini
R
UC
LC
HAEMATOPHAGOUS PARASITES
HAEMOLYMPHOPHAGOUS PARASITES
POLLINOPHAGOUS
NECTAROPHAGOUS
INSECTIVOROUS PREDATORS

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Continental Drift Events

PRESENT DAY

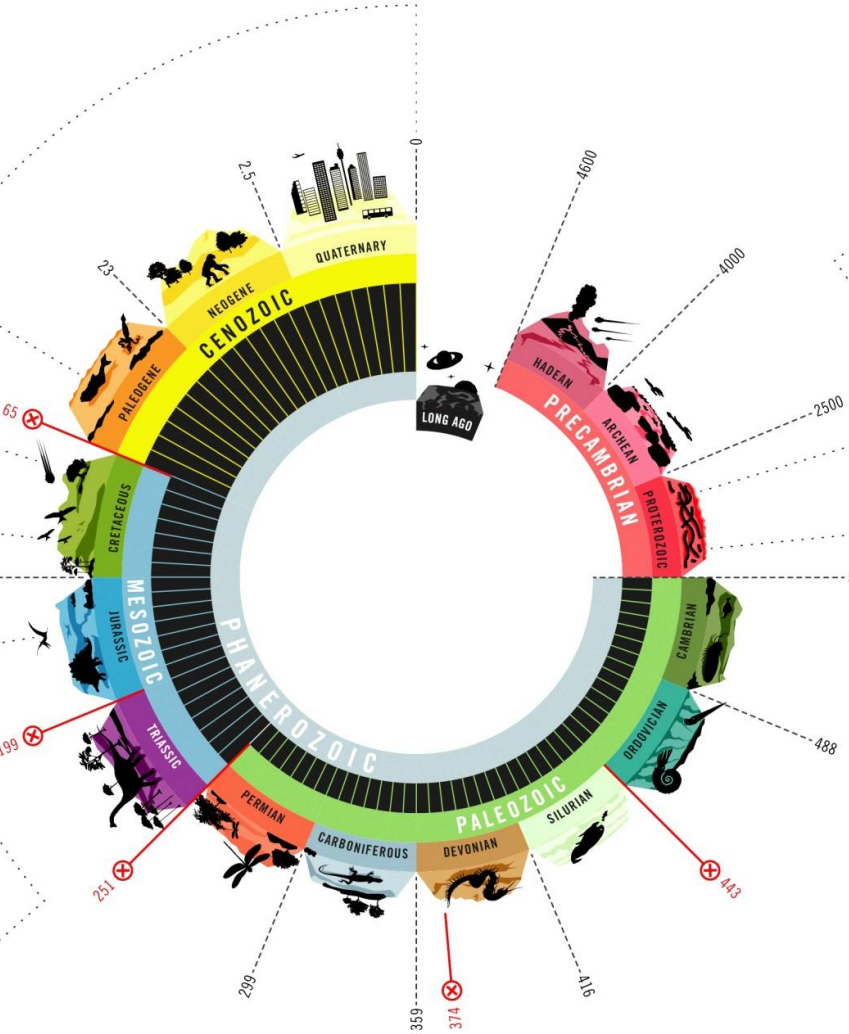
Circa 40 Million years ago

Circa 80 Million years ago

Circa 120 Million years ago

Circa 160 Million years ago

PANGEA
Circa 200 Million years ago

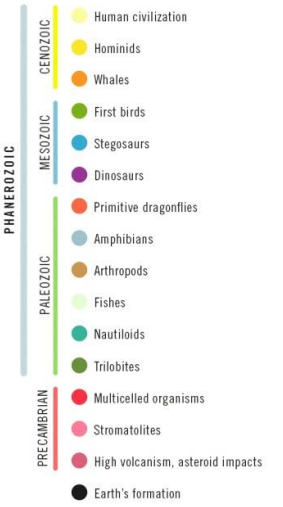


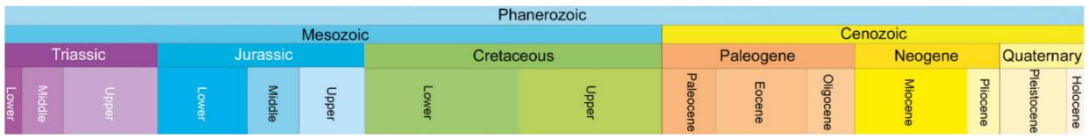
COLUMBIA
Circa 1800 Million Years ago

RODINIA
Circa 800 Million years ago

PANNOTIA
Circa 550 Million years ago

Milestones





Diptera — Culicomorpha — biting midges — mosquitoes

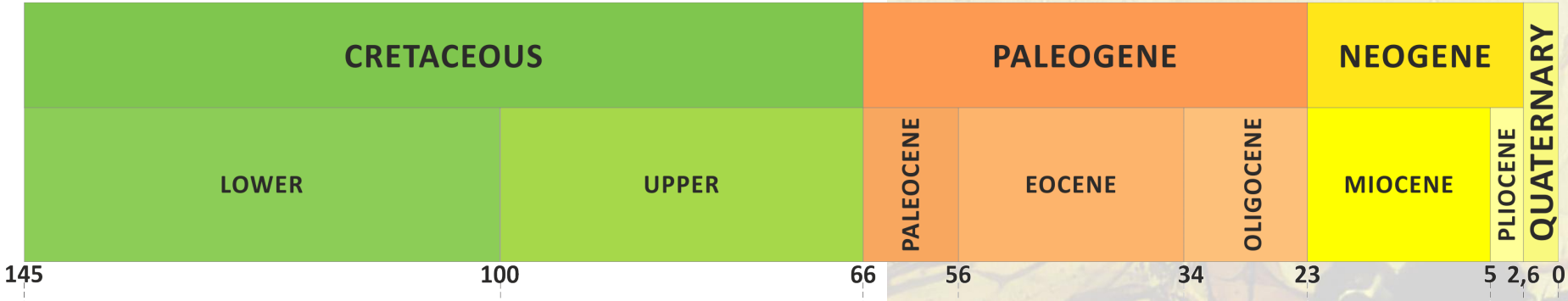
*after Infographics: The History of Life, changed.

The oldest known member
of the genus *Culicoides*
(Upper Cretaceous, 100 Ma)

The new *Culicoides* species has been found in Burmese amber (Upper Cretaceous, 100 Ma)

- Female specimen
- Abdomen missing
- Sensilla coeloconica numerous, but present only on first flagellomere
- Third palpal segment without sensory pit
- Wing membrane covered with macrotrichia

Previously, the oldest record belonged to *C. doyeni* Choufani et al. 2014, described from French amber of Vendée (Upper Cretaceous, 95-85 Ma).



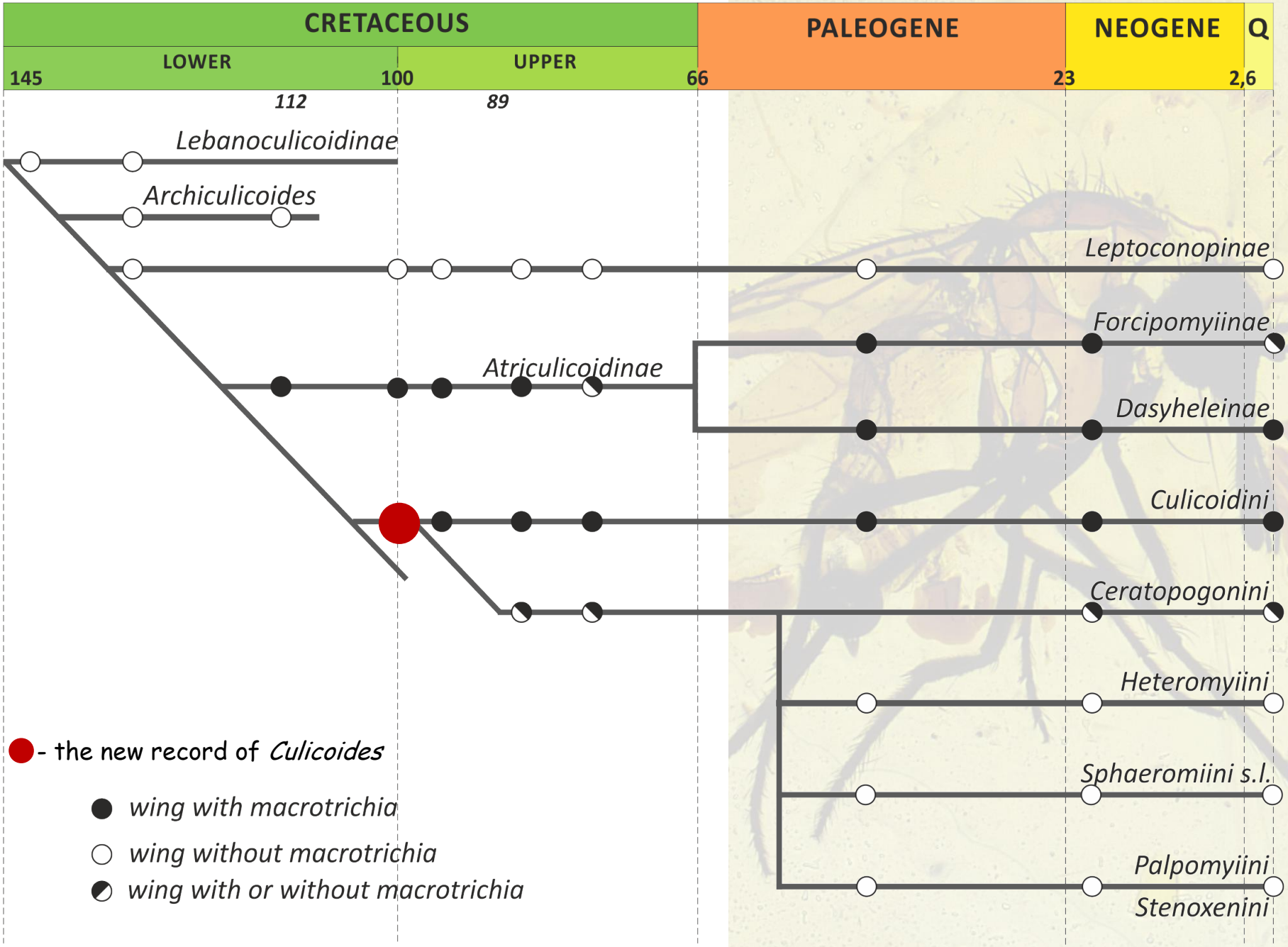
Lebanoculicoides
Archiaustroconops

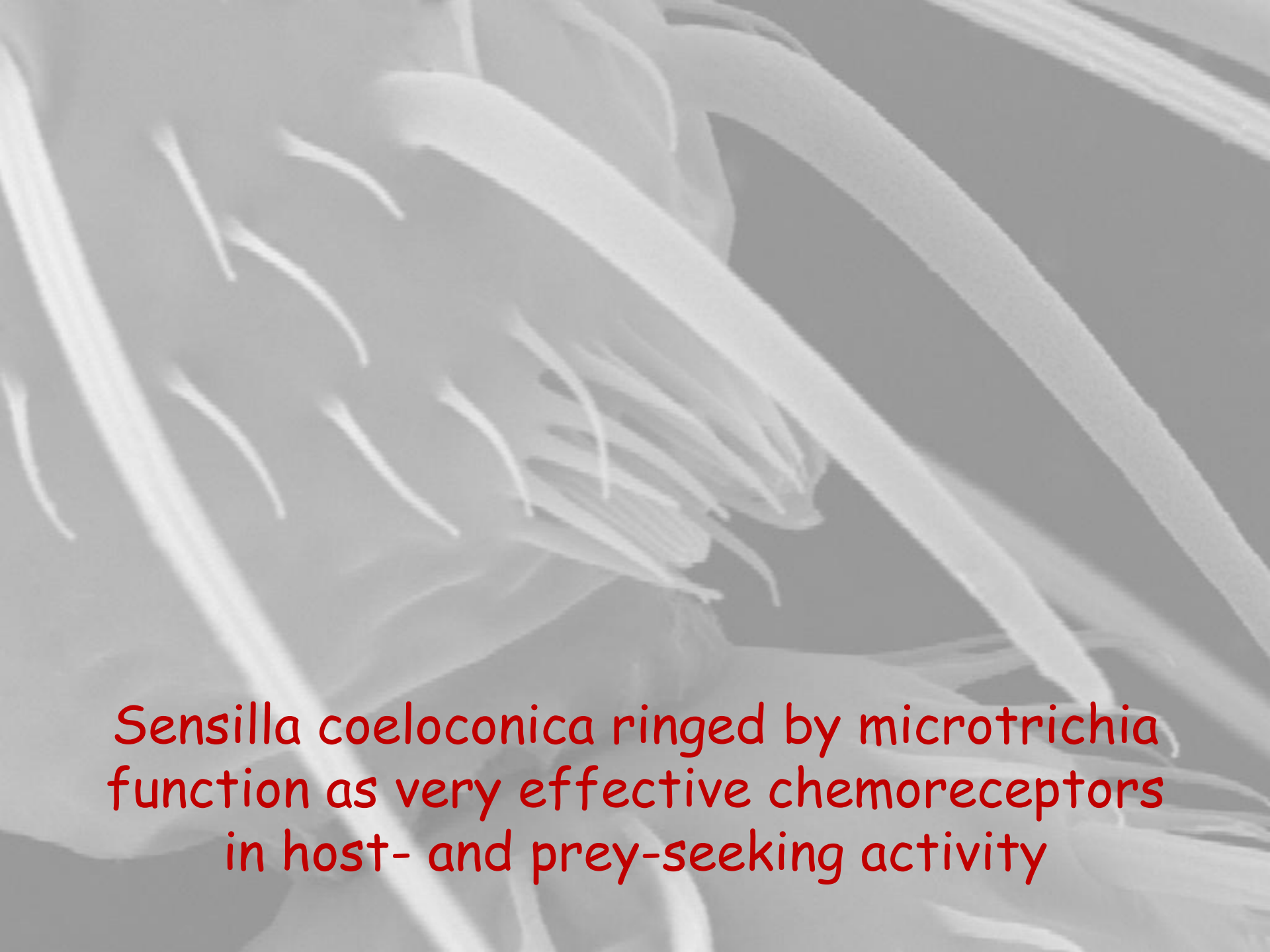
Leptoconops, *Austroconops*

Culicoides

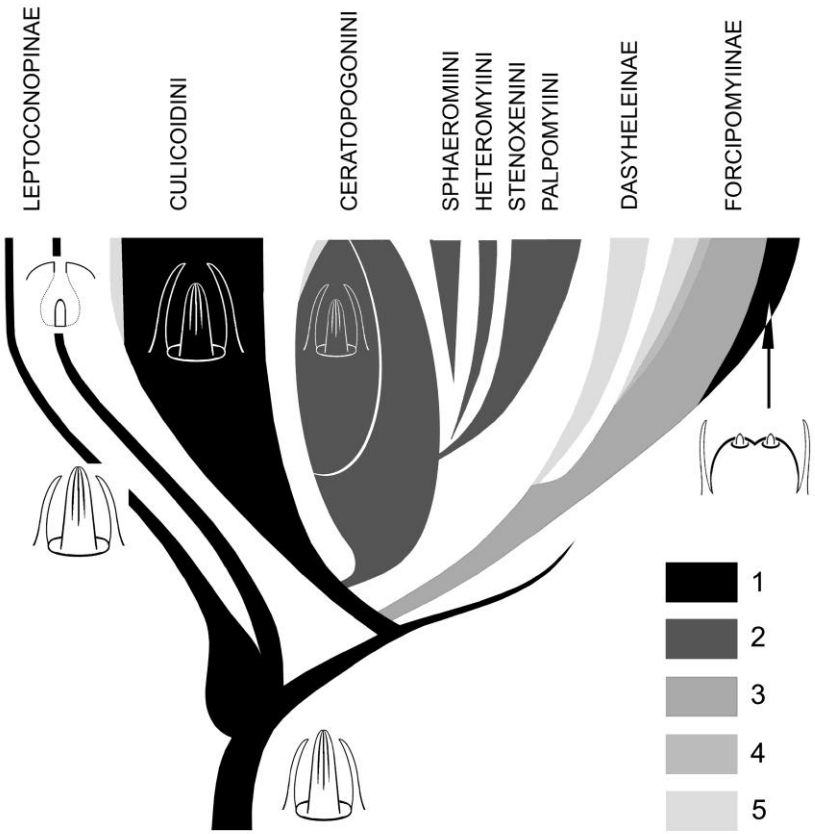
Forcipomyia (*Lasiohelea*)

Among all groups of Culicomorpha, only some species of ceratopogonids and chironomids have wing membrane covered with macrotrichia


CRETACEOUS
PALEOGENE
NEOGENE
Q
LOWER
UPPER
145
100
66
23
2,6
112
89
Lebanoculicoidinae
Archiculicoides
Leptoconopinae
Forcipomyiinae
Atriculicoidinae
Dasyheleinae
Culicoidini
Ceratopogonini
Heteromyiini
Sphaeromiini s.l.
Palpomyiini
Stenoxenini
- the new record of Culicoides
wing with macrotrichia
wing without macrotrichia
wing with or without macrotrichia



Sensilla coeloconica ringed by microtrichia function as very effective chemoreceptors in host- and prey-seeking activity



Evolution of female feeding habits and distributions of sensilla coeloconica ringed by microtrichia in the main groups of biting midges

(1) haematophagous parasites feeding on vertebrates
(2) insectivorous predators
(3) haemolymphophagous parasites
(4) pollinophagous feeders
(5) nectarophagous feeders

Genus	No. of antennal flagellomeres					Type of meal/activity
	1	2-8	9-12	2-12	13	
Basal lineage † *Archiculicoides*		-	-	-	-	blood of vertebrates ☾ ?
Leptoconopinae						
Austroconops		-	-	-	-	blood of vertebrates ☼ ☾
Leptoconops		-	-	-	-	blood of vertebrates ☼
Forcipomyiinae						
Forcipomyia (*Lasiohelea*)	-	-	-	-		blood of vertebrates ☾
Forcipomyia (other subgenera)	-	-	-	-		nectar, haemolymph ☾
Atrichopogon	-	-	-	-		nectar, haemolymph ☾
Ceratopogoninae						
Culicoidini						
Culicoides						blood of vertebrates ☾
		-	-	-	-	
			-	-	-	
		-		-	-	
Paradasyhelea		-		-	-	no protein meal ☾
	-		-	-	-	
			-	-	-	
Ceratopogonini		-	-	-	-	predators on insects ☾
			-	-	-	

Thank you
for your attention!