Ecological and evolutionary history of Ochyromerini weevils: insights into the emergence of brood-site pollination in the tropics

Histoire évolutive et écologique des charançons Ochyromerini : vers une compréhension de l'émergence des systèmes de pollinisation de couvain en zone tropicale

Benjamin ZELVELDER

Supervisor: **Rémi Allio, Julien Haran**

Direction: **Benoit Nabholz**

Affiliation: **ISEM, Université de Montpellier, UMR CBGP**

Introduction

Introduction

R. Allio & B. Zelvelder

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Introduct

R. Allio & B. Zelvelder











R. Allio & B. Zelvelder

Reconstructing the evolutionary history

Reconstructing the evolutionary history

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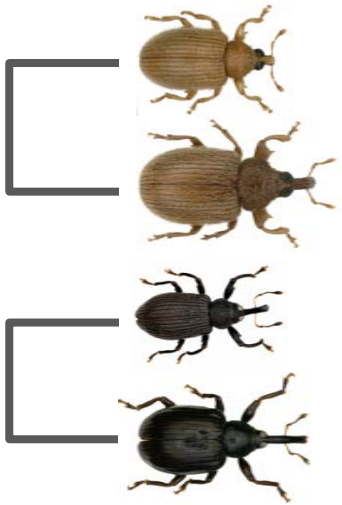
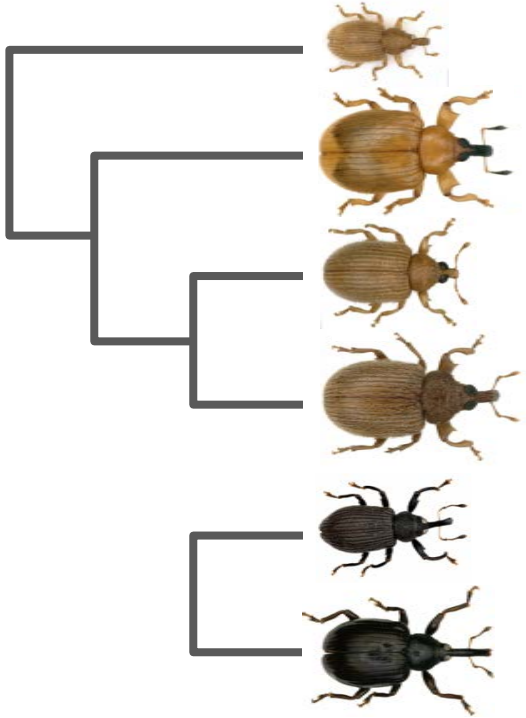
Reconstructing the evolutionary history

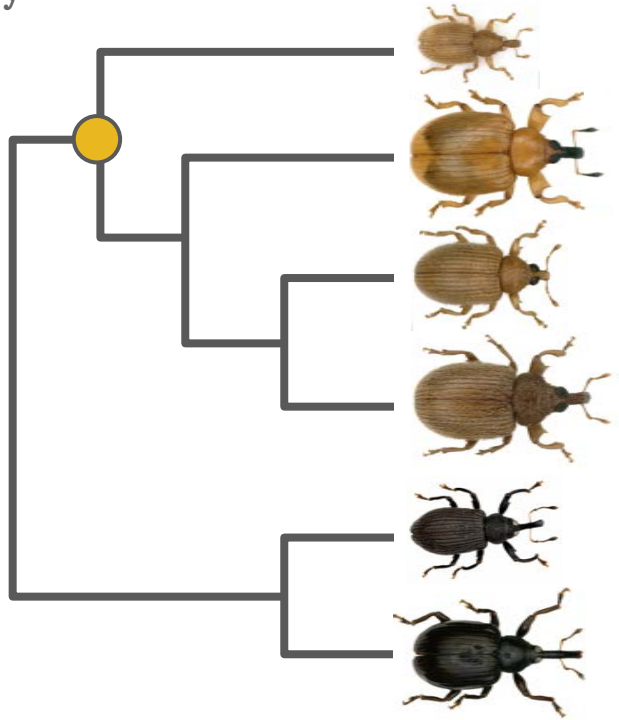


Reconstructing the evolutionary history



Reconstructing the evolutionary history

Phylogeny

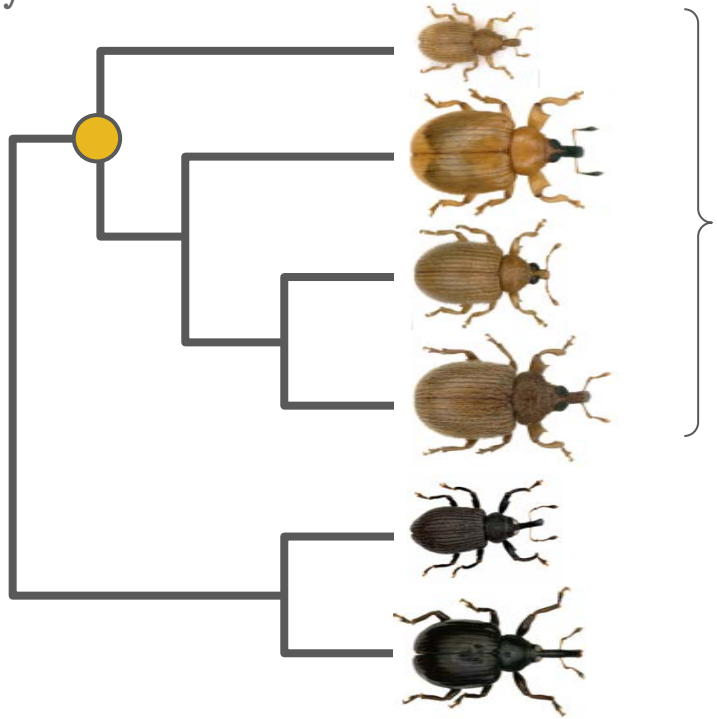


“Clade”

Most recent common ancestor

Reconstructing the evolutionary history

Phylogeny



Lifestyle?

Region?

Morphological trait?

Most recent common ancestor

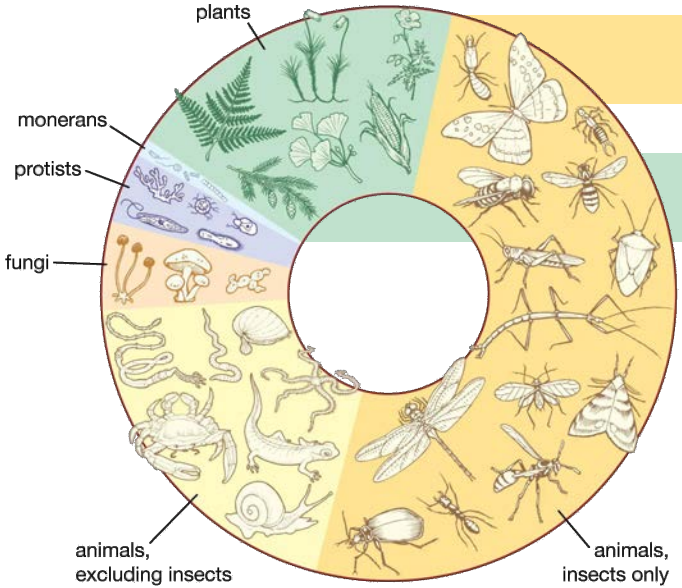
The weevil superfamily

"Curculionoidea"

R. Allio & B. Zelvelder

The weevil superfamily

"Curculionoidea"



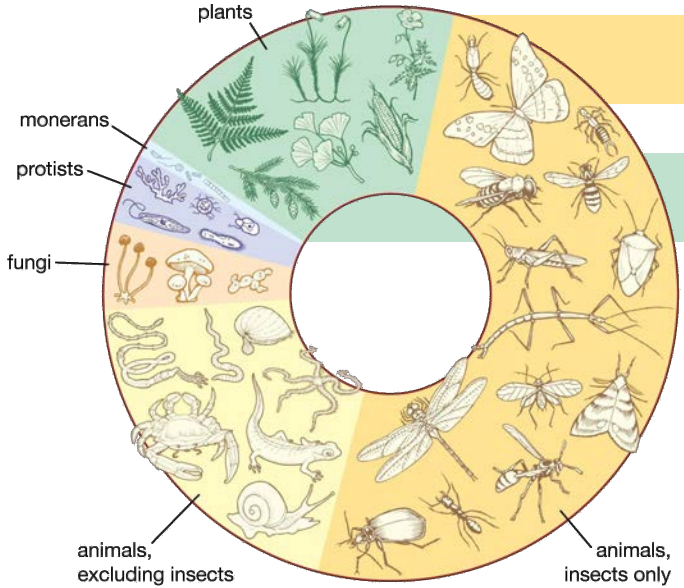
~1M Insects

~300k Plants

R. Allio & B. Zelvelder

The weevil superfamily

"Curculionoidea"



~1M Insects

~300k Plants

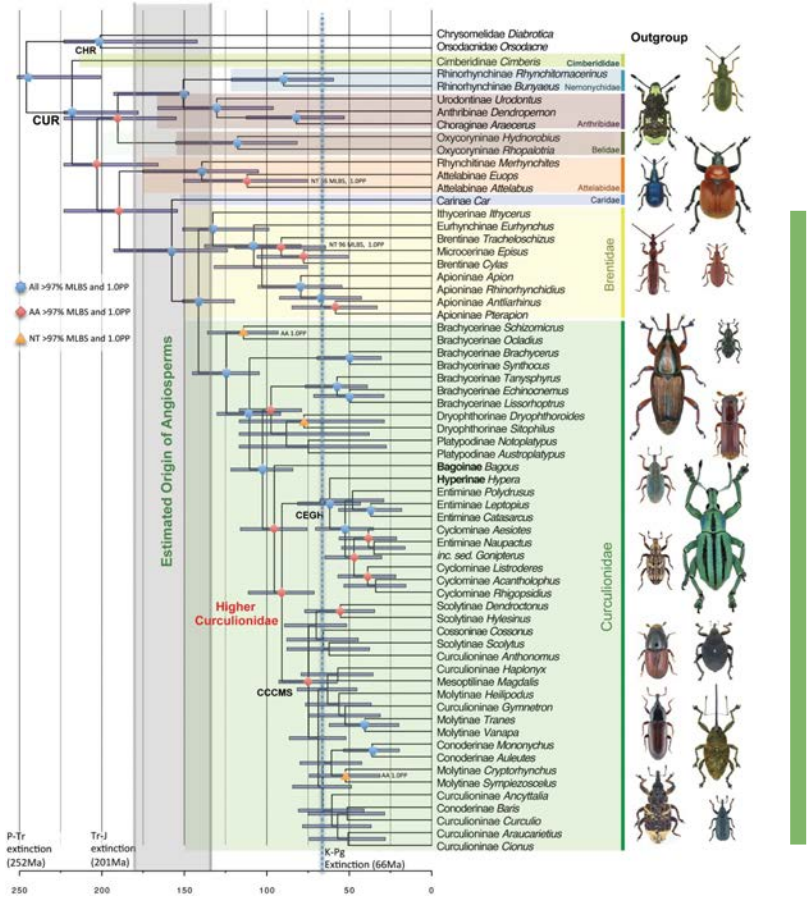
~400k Coleoptera

~62k Weevils

~220k estimated

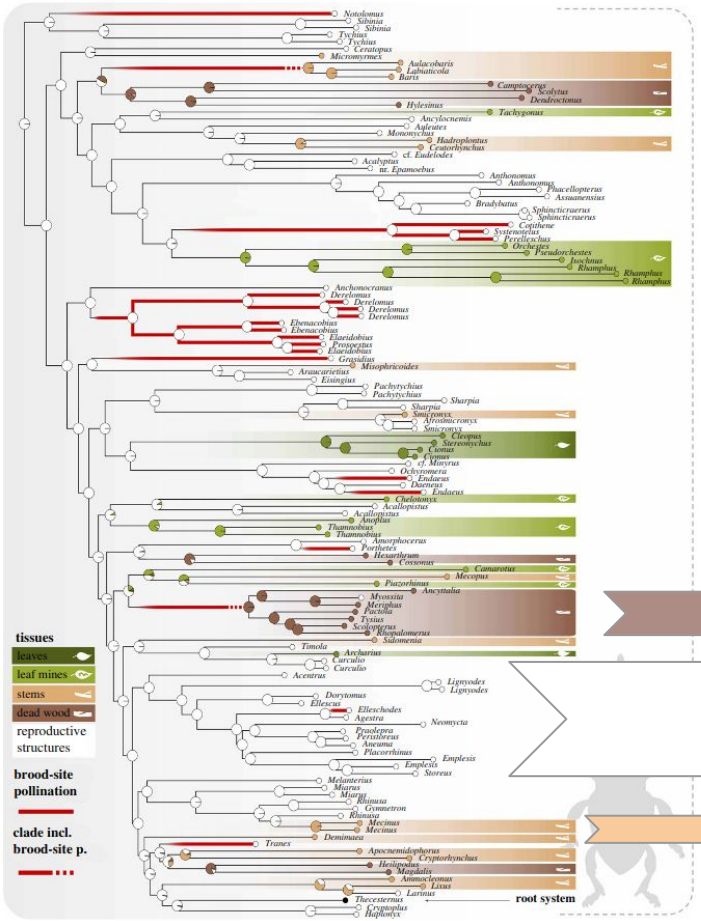
Oberprieler et al. 2007

R. Allio & B. Zelvelder



Shin et al. 2018 - Phylogenetic tree of weevils

- Co-diversification with flowering plants (Angiosperms)



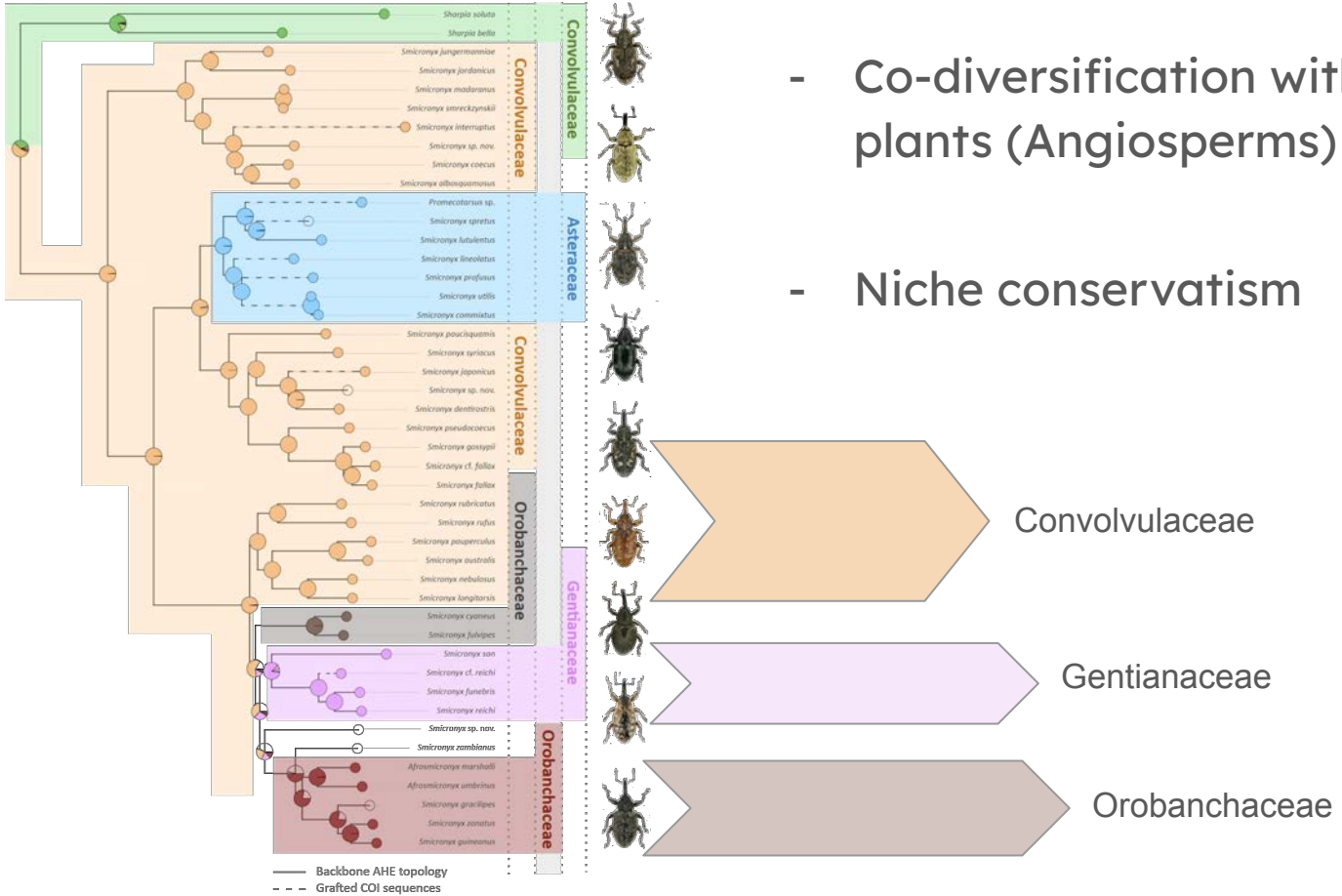
- Co-diversification with flowering plants (Angiosperms)
- Niche conservatism

Dead wood

Reproductive structures

Stems

Haran et al. 2023b - Phylogenetic tree of weevils



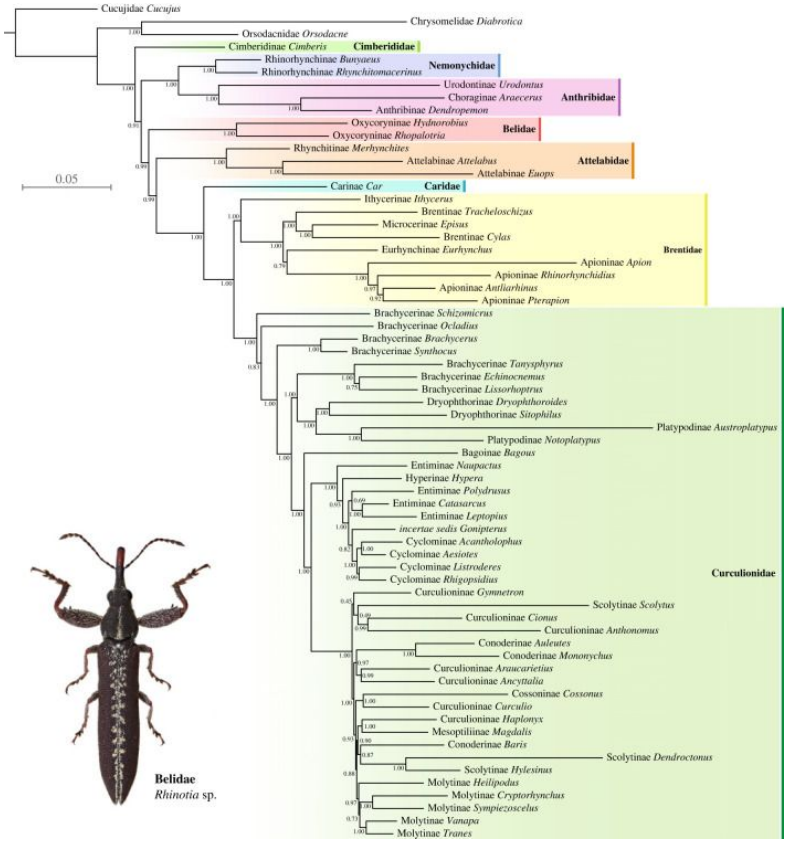
- Co-diversification with flowering plants (Angiosperms)
- Niche conservatism

Convolvulaceae

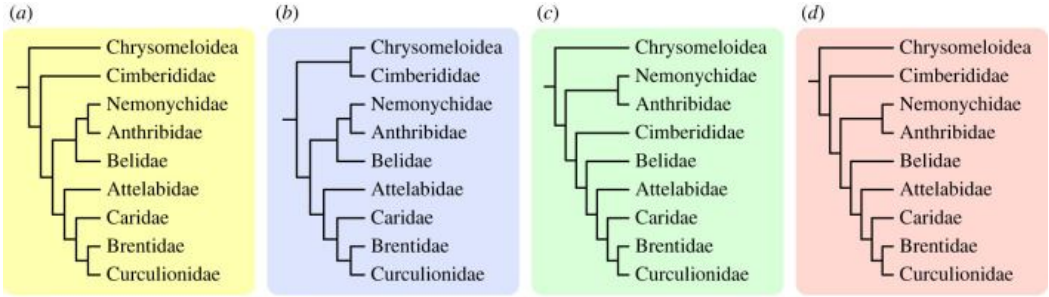
Gentianaceae

Orobanchaceae

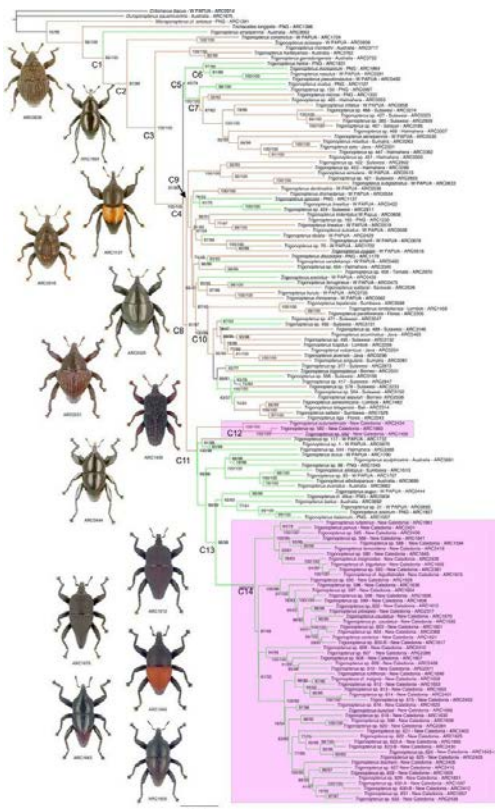
Zelvelder et al. 2026 - Phylogenetic tree of Smicronychini tribe



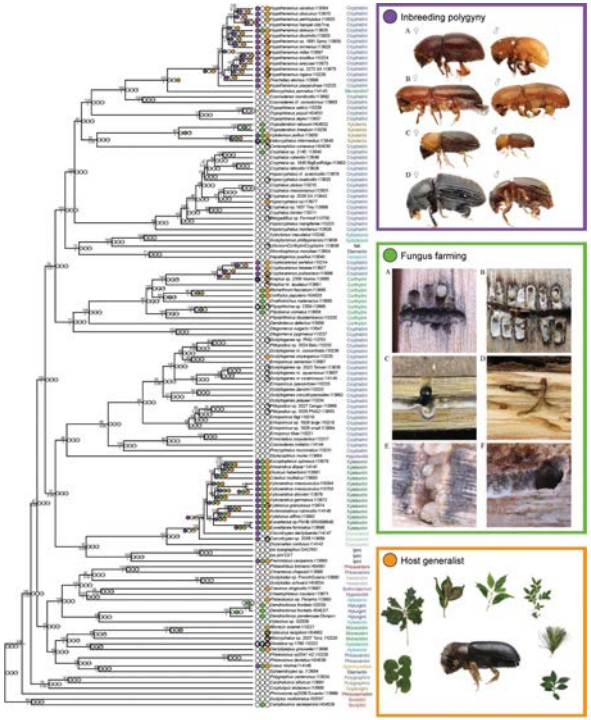
Hard to resolve systematic classification



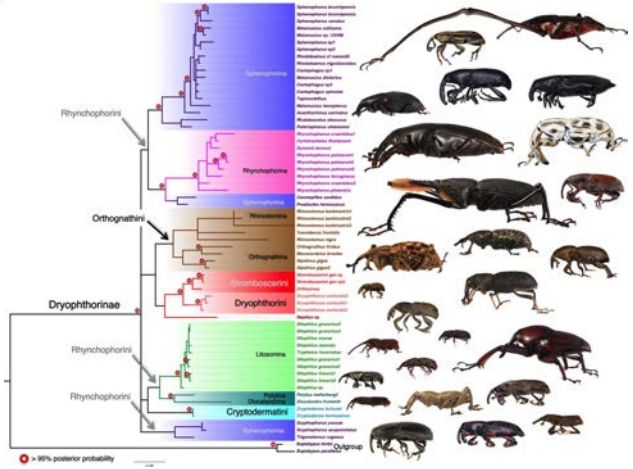
Li et al. 2023 - Phylogenetic tree of weevils



Toussaint et al. 2017 - *Trigonopterus*

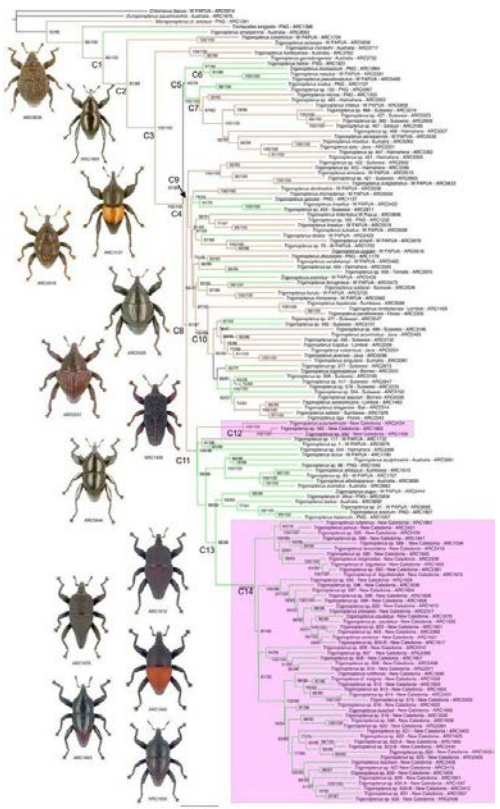


Johnson et al. 2018 - Scolytinae

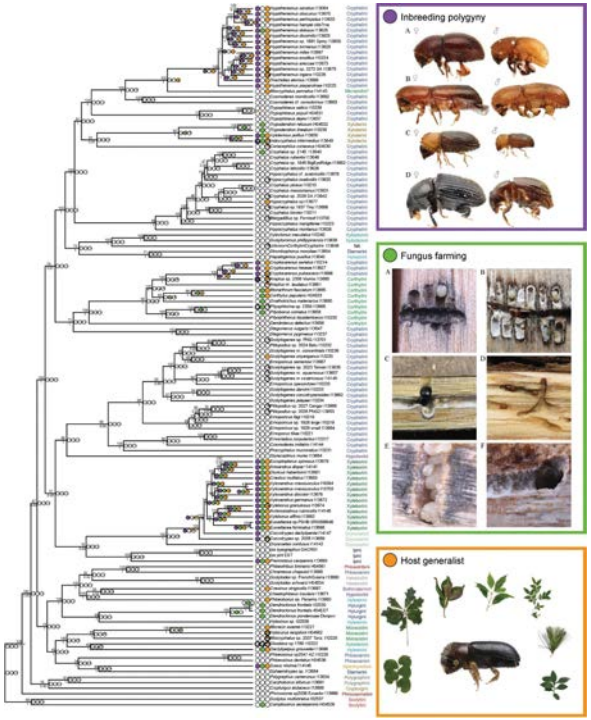


Chamorro et al. 2021 - Dryophtorinae

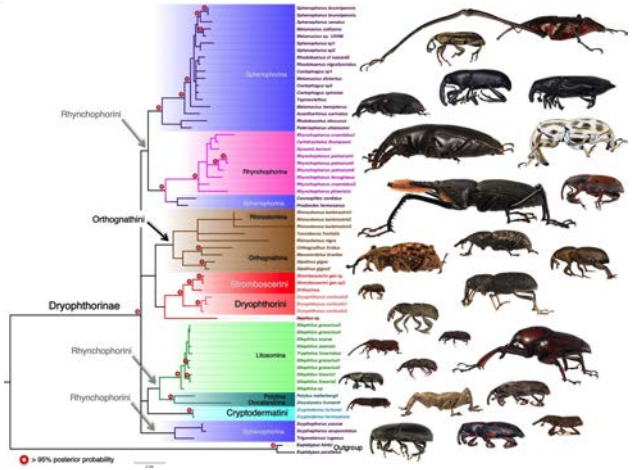
Few phylogenetic studies



Toussaint et al. 2017 - *Trigonopterus*



Johnson et al. 2018 - Scolytinae



Chamorro et al. 2021 - Dryophtorinae

B. de Medeiros

Antagonism and mutualism

among weevils

@exonie

Antagonism and mutualism

among weevils

@bsteer

@gillessanmartin

Antagonism and mutualism

among weevils

@bsteer

@gillessanmartin

B. de Medeiros

Nunes et al. 2018
Haran et al. 2021, 2022, 2023a-b
Hsiao et al. 2023, Dao et al. 2023
Rocamundi et al. 2024
Ibañez et al. 2025, Haran et al. 2025
Haran et al. 2026, De Meideros et Perris 2026, Wu et Chen 2026

Antagonism and mutualism

among weevils

@bsteer

@gillessanmartin

Haran et al. 2023a

Pollination by weevils

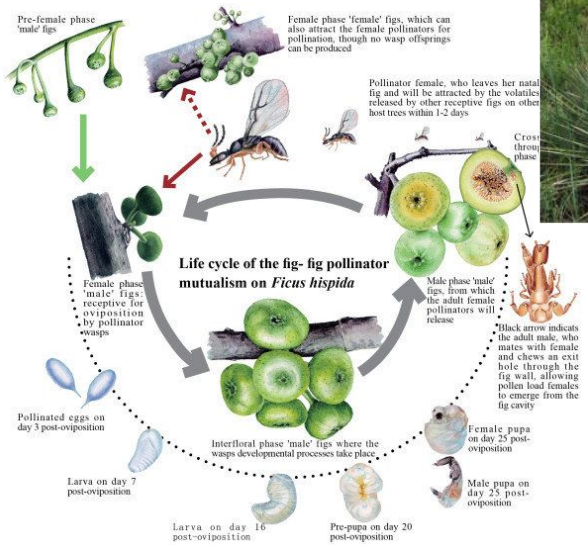
= Brood-site pollination

- Visiting flowers to lay their eggs and feed their larvae

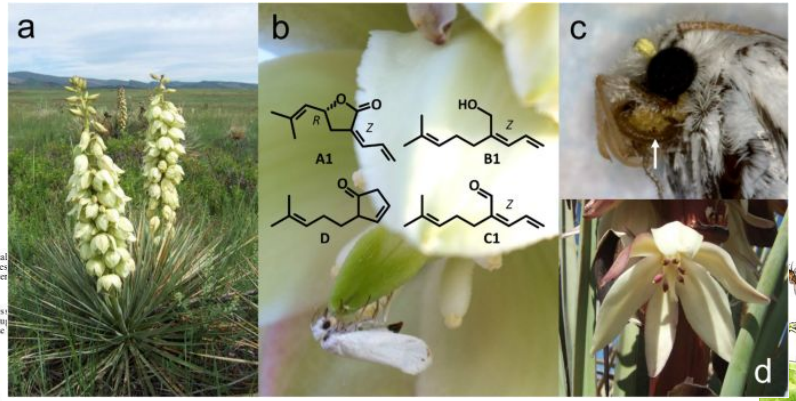
B. Zelvelder

Brood-site pollination mutualism

Fig-Fig wasps



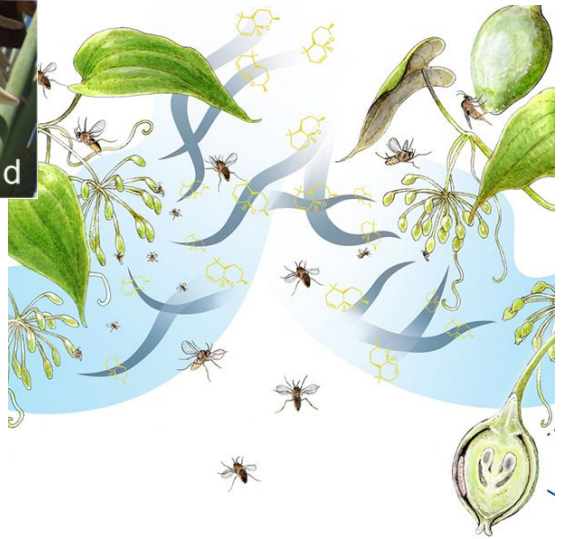
Xiao et al. 2013 - Hymenoptera, Agaonidae



Tröger et al. 2013 - Lepidoptera, Prodoxidae

Yukka-Yukka moths

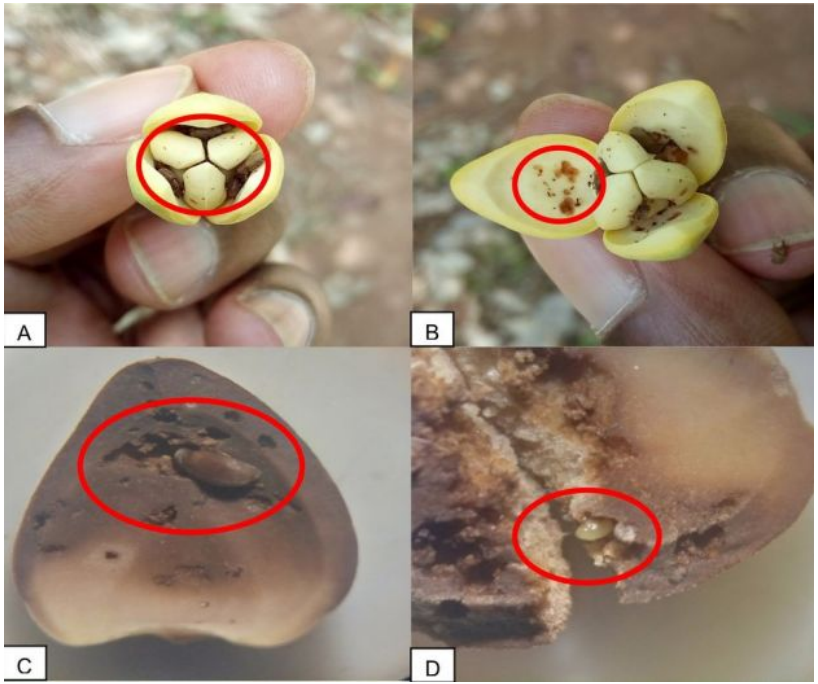
Cecidomyiid flies



Suetsugu et al. 2026 - Diptera, Cecidomyiidae

Brood-site pollination mutualism

- Evolution of a trade-off between plant tissue **consumption** and **pollination**



Dao et al. 2023

Brood-site pollination mutualism

- Evolution of a trade-off between plant tissue **consumption** and **pollination**

  = When **pollen limitation** is high and plants **population density** is low

Brood-site pollination mutualism

- Evolution of a trade-off between plant tissue **consumption** and **pollination**

  = When **pollen limitation** is high and plants **population density** is low

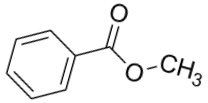
  = Through **host specificity**

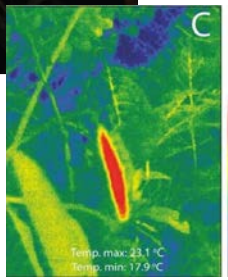
Sakai 2002, Haran et al. 2023a

Brood-site pollination by weevils

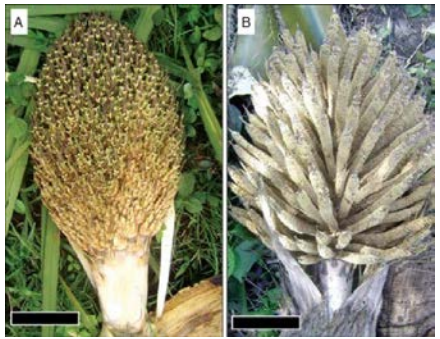
Floral traits of the **Cantharophilous/Ciophilous** pollination syndrome:

- Fleshy tissues
- Odorant volatile compounds
- Thermogenesis
- Dioecy
- …





Ibañez et al. 2025



♀ ♂

Silberbauer-Gottsberger et al. 2003, Hsiao et al. 2023

Adam et al. 2011

Brood-site pollination by weevils

Floral traits of the **Cantharophilous/Ciophilous** pollination syndrome:

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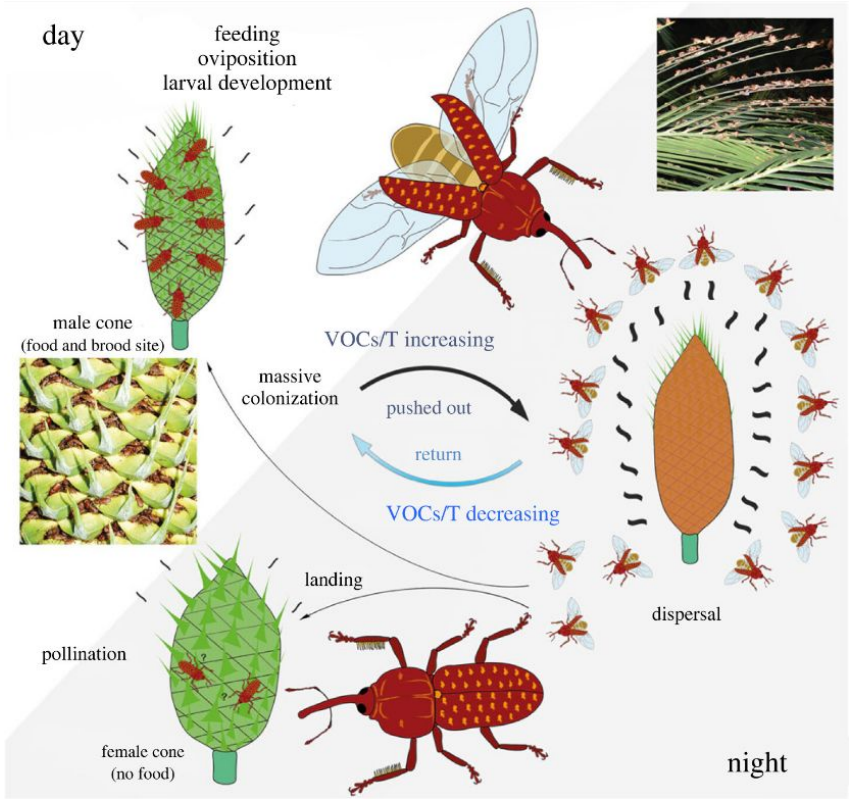


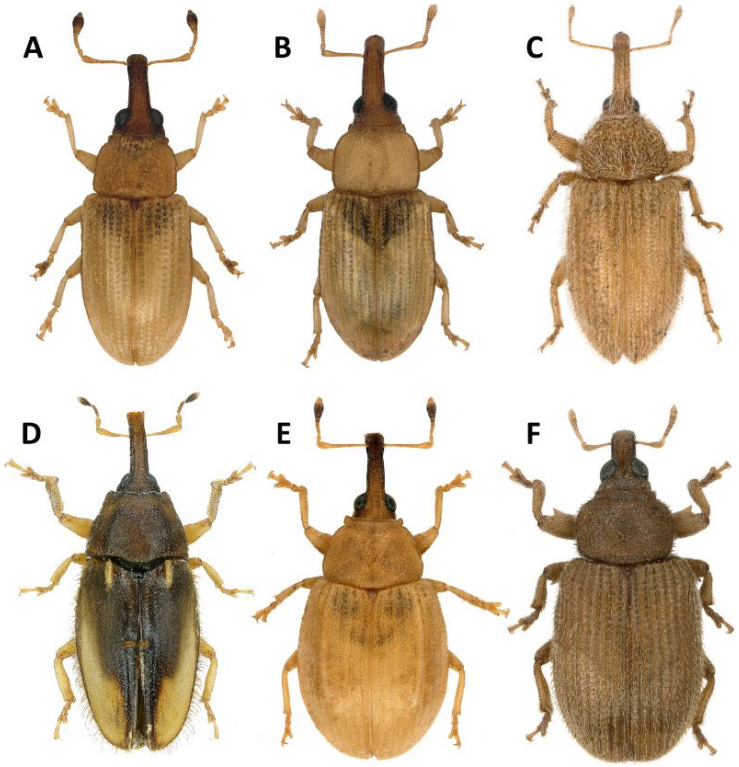
Hsiao et al. 2023

Silberbauer-Gottsberger et al. 2003, Hsiao et al. 2023

Brood-site pollination by weevils

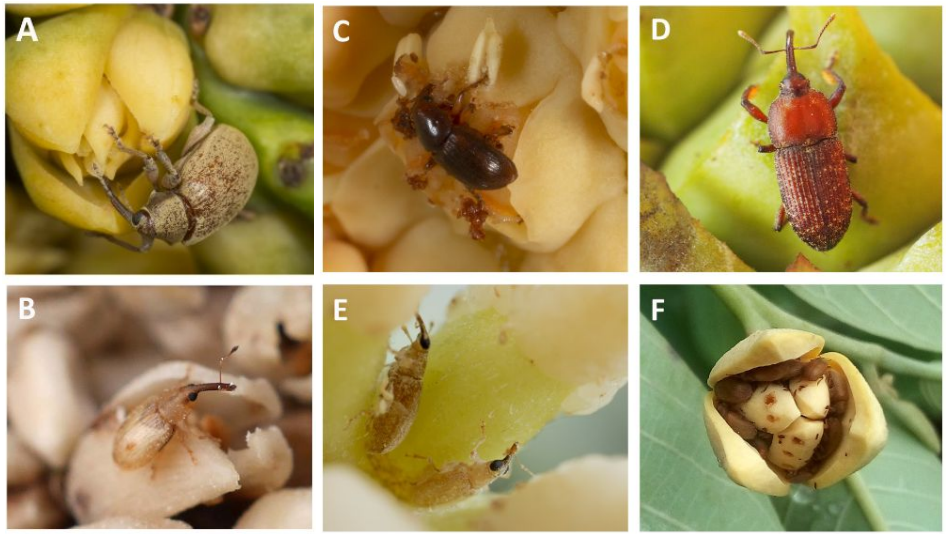
“Morphotype” of pollinating weevils:

- Small size
- Reddish-yellowish color
- Good flight capacity
- Thin hairs
- …



Haran et al. 2023a

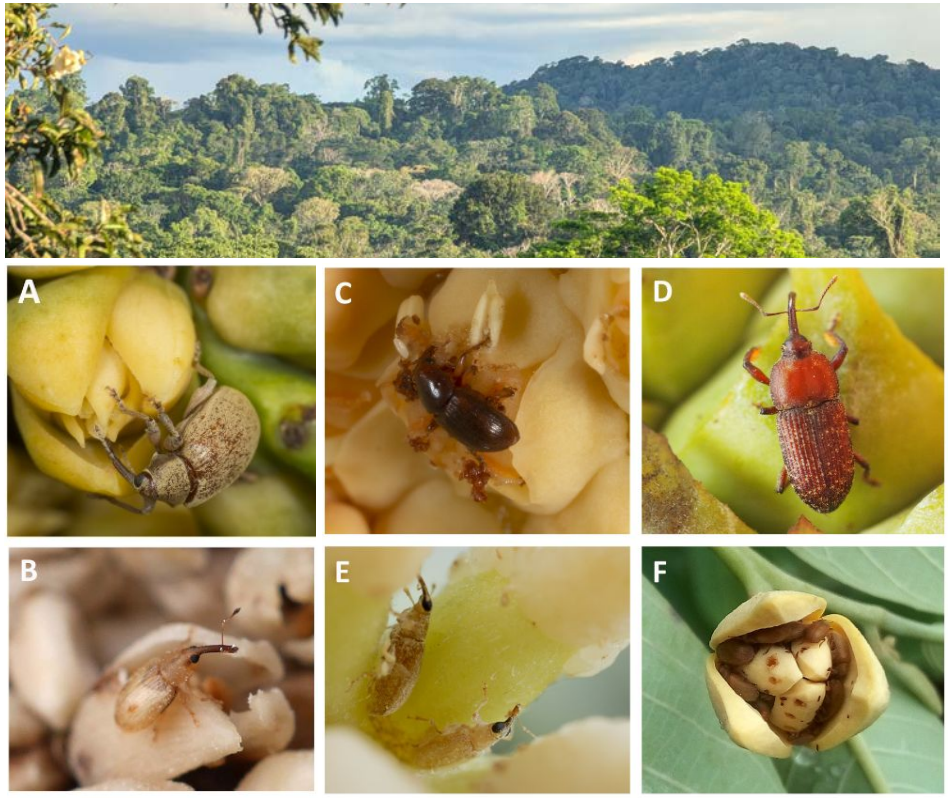
Brood-site pollination by weevils



- Numerous **morphological** and **ecological traits** in both plants and weevils

Haran et al. 2023a

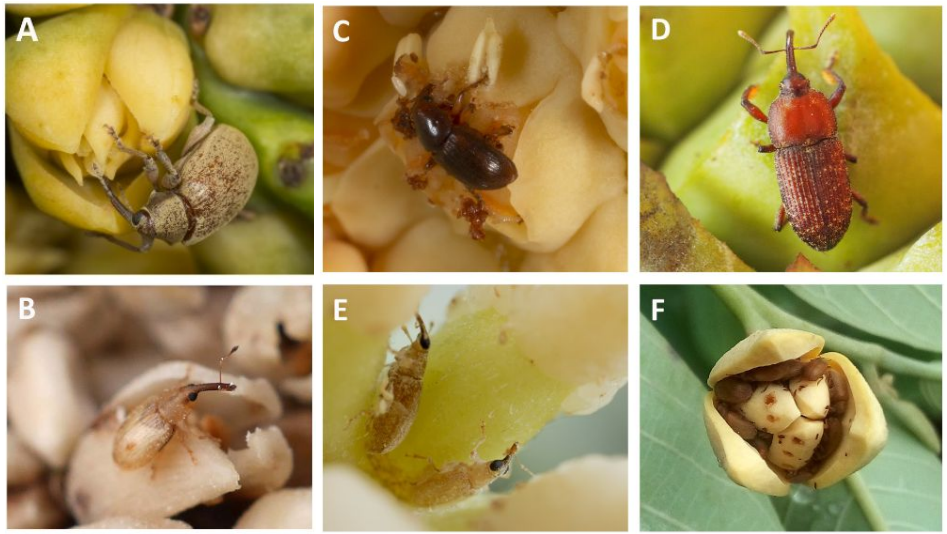
Brood-site pollination by weevils



- Numerous **morphological** and **ecological traits** in both plants and weevils
- Especially favored in **tropical** regions

Haran et al. 2023a

Brood-site pollination by weevils



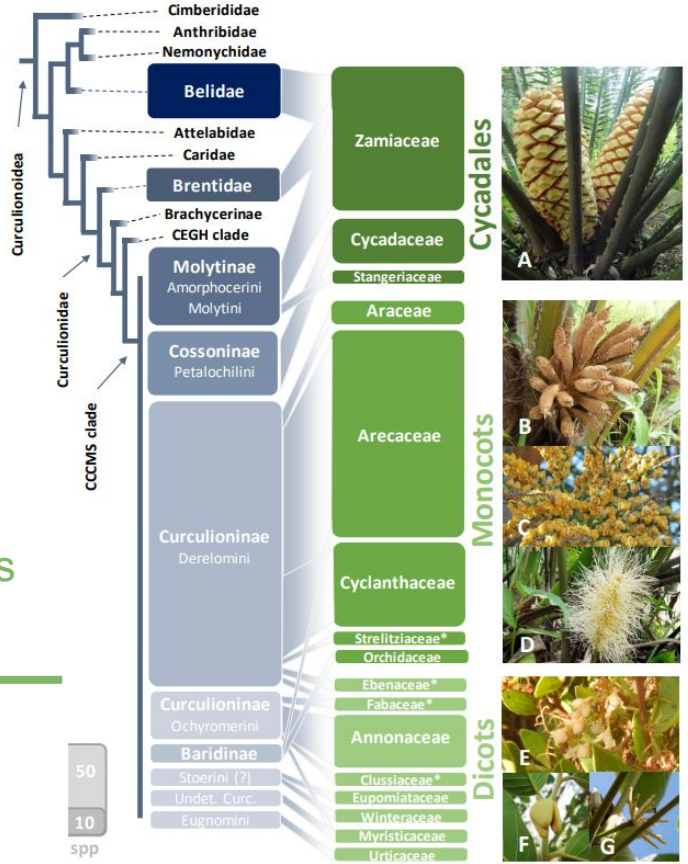
- Numerous **morphological** and **ecological traits** in both plants and weevils
- Especially favored in **tropical** regions
- **Overlooked** due to a long-standing paradigm

Haran et al. 2023a

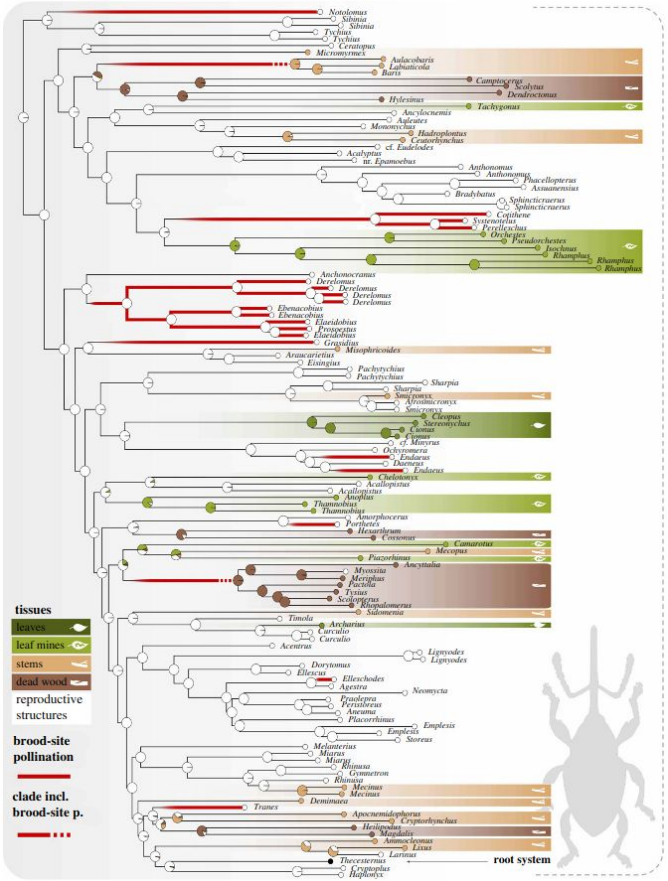
Plant families involved

x16

…and much more to discover



Haran et al. 2023a



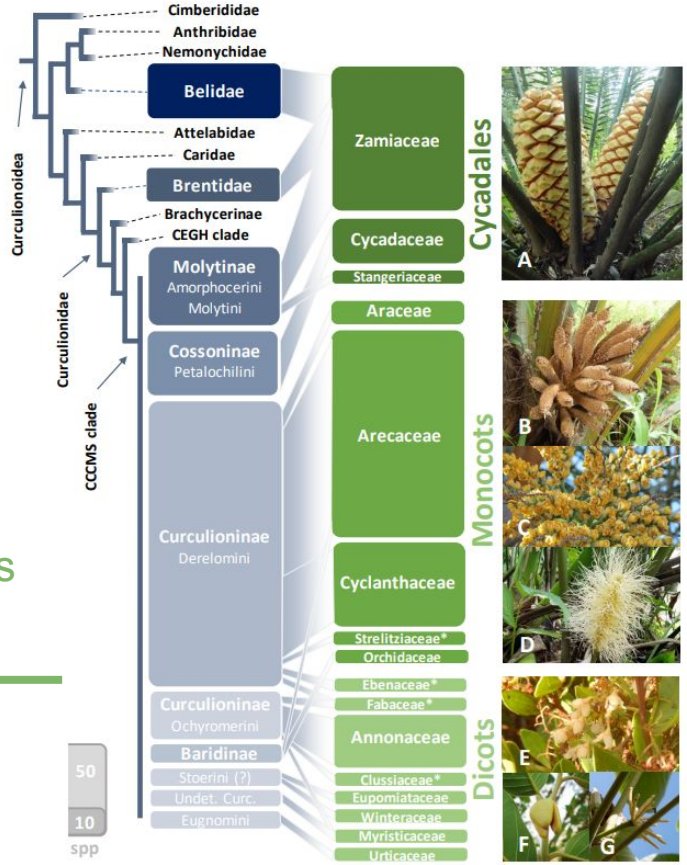
Haran et al. 2023b

Pollinating weevil lineages

x12

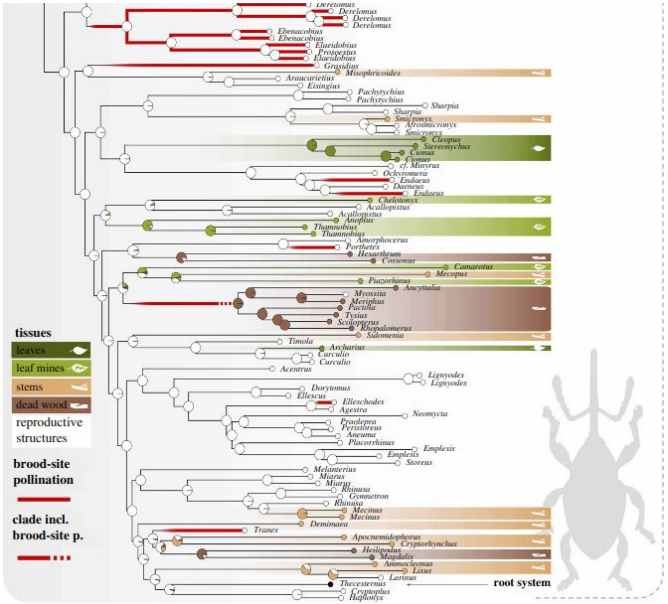
Plant families involved

x16



Haran et al. 2023a

Ecological and evolutionary history of Ochyromerini weevils: **insights into the emergence of brood-site pollination in the tropics**

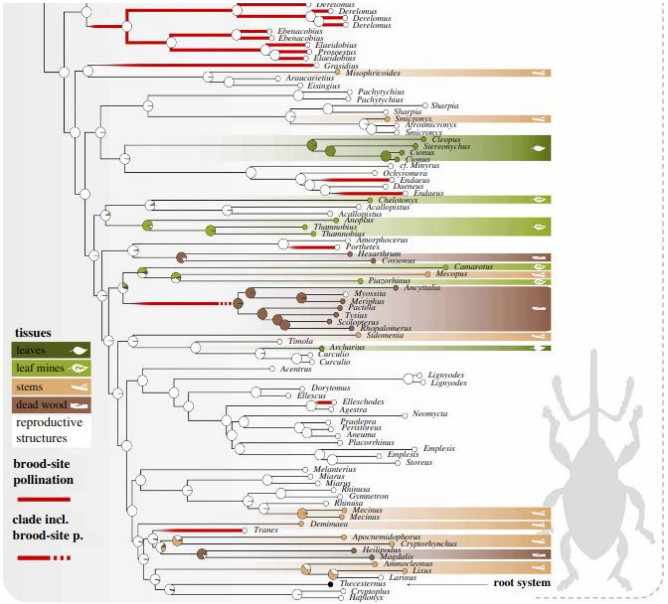


Haran et al. 2023b

Pollinating weevil lineages
x12

Unique pattern of **repeated evolution** towards mutualism

Ecological and evolutionary history of *Ochyromerini* weevils: insights into the emergence of brood-site pollination in the tropics



Haran et al. 2023b

Pollinating weevil lineages

x12

Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

+

- Both **mutualist** and **antagonist** species


Ligustrum spp. (Oleaceae), *Ochyromera ligustri*


Annona senegalensis (Annonaceae), *Endaeus castus*

Dao et al. 2023

Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

+

- Both **mutualist** and **antagonist** species
- Numerous **host plant families**


Phyllanthaceae (*Glochidion*)


Schisandraceae (*Illicium*)


Fabaceae (*Baikiaea*)


Sapotaceae (*Mimusops*)


Pinaceae (*Tsuga*)


Clusiaceae (*Allanblackia*)


Annonaceae (*Annona*)


Theaceae (*Schima*)

Kojima, Marshall, Miwa, Momose, Morimoto, Oberprieler, Voss, Wray…

Order: Coleoptera
Family: Curculionidae

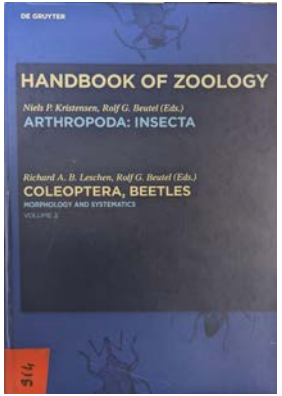
Tribe: **Ochyromerini**

+

- Both **mutualist** and **antagonist** species
- Numerous **host plant families**

–

- Very **poorly known** and inaccessible knowledge



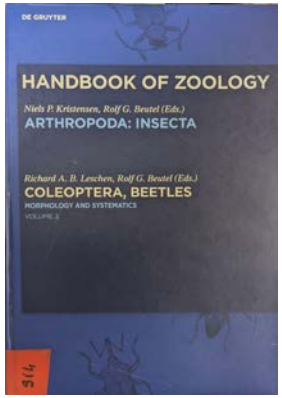
\+ Oberprieler 2003 (Afrique)

\+ Kojima 1995a-f,1996a-b (Asie)

Caldara et al. 2014

Order: Coleoptera
Family: Curculionidae

Tribe: **Ochyromerini**



\+ Oberprieler 2003 (Afrique)

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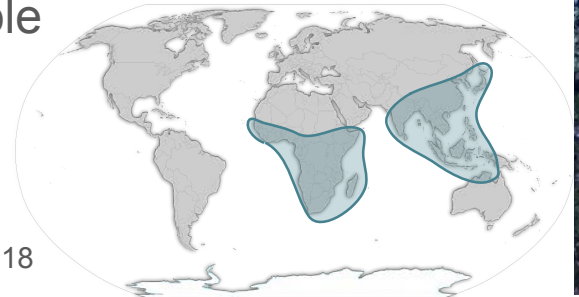
Caldara et al. 2014

+

- Both **mutualist** and **antagonist** species
- Numerous **host plant families**

–

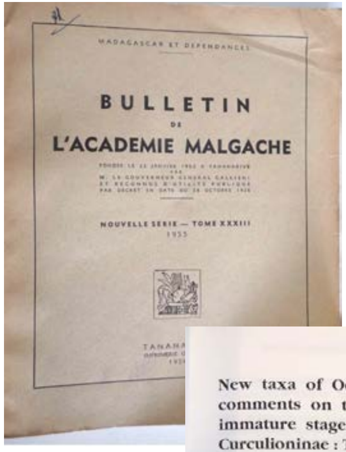
- Very **poorly known** and inaccessible knowledge
- Difficult to sample, although **very abundant**



Sprick et Floren 2018

Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

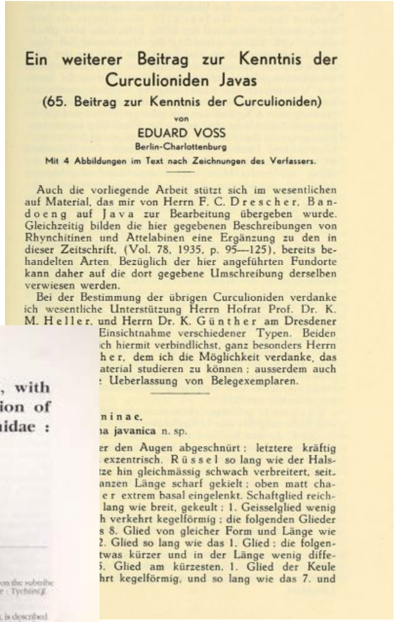
Bibliographic synthesis


MADAGASCAR ET DÉPENDANCES

BULLETIN
DE
L'ACADÉMIE MALGACHE

NOUVELLE SÉRIE — TOME XXXIII
1955

TANANA...

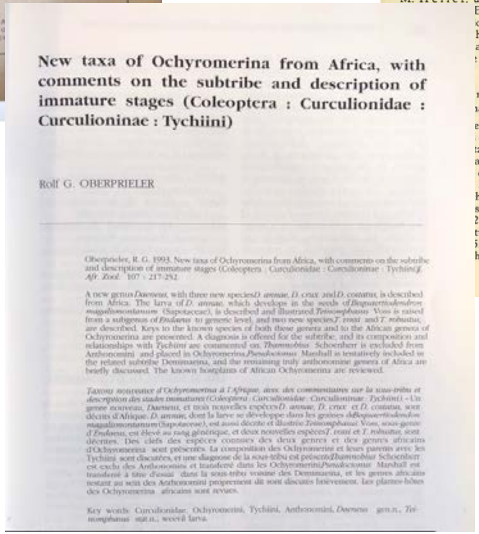

Ein weiterer Beitrag zur Kenntnis der Curculioniden Javas
(65. Beitrag zur Kenntnis der Curculioniden)
von
EDUARD VOSS
Berlin-Charlottenburg
Mit 4 Abbildungen im Text nach Zeichnungen des Verfassers.

Auch die vorliegende Arbeit stützt sich im wesentlichen auf Material, das mir von Herrn F. C. Drescher, Bandoeng auf Java zur Bearbeitung übergeben wurde. Gleichzeitig bilden die hier gegebenen Beschreibungen von Rhynchitinen und Attelabinen eine Ergänzung zu den in dieser Zeitschrift, (Vol. 78, 1935, p. 95—125), bereits behandelten Arten. Bezüglich der hier angeführten Fundorte kann daher auf die dort gegebene Umschreibung derselben verwiesen werden.

Bei der Bestimmung der übrigen Curculioniden verdanke ich wesentliche Unterstützung Herrn Hofrat Prof. Dr. K. M. Heller, und Herrn Dr. K. Günther am Dresdener ... Einsichtnahme verschiedener Typen. Beiden ...ch hiermit verbindlichst, ganz besonders Herrn ...her, dem ich die Möglichkeit verdanke, das ...aterial studieren zu können; ausserdem auch ... Ueberlassung von Belegexemplaren.

...ninae.
...a javanica n. sp.

...er den Augen abgeschnürt; letztere kräftig ... exzentrisch. Rüssel so lang wie der Hals... ...ze hin gleichmässig schwach verbreitert, seit... ...anzen Länge scharf gekielt; oben matt cha... ...er extrem basal eingelenkt. Schaftglied reich... ... lang wie breit, gekeult; 1. Geisselglied wenig ...h verkehrt kegelförmig; die folgenden Glieder ...s 8. Glied von gleicher Form und Länge wie ...2. Glied so lang wie das 1. Glied; die folgen... ...twas kürzer und in der Länge wenig diffe... ...5. Glied am kürzesten. 1. Glied der Keule ...hrt kegelförmig, und so lang wie das 7. und

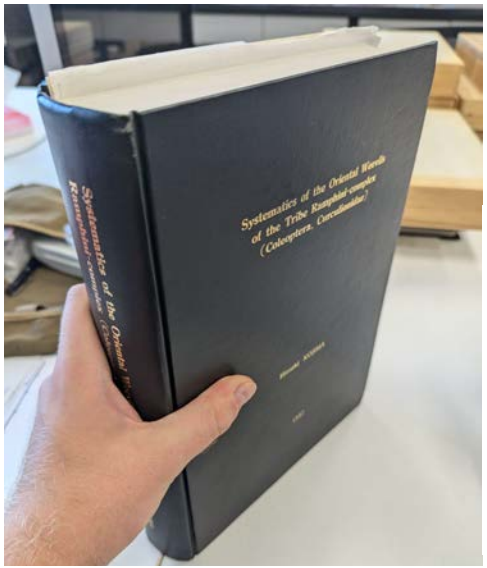

New taxa of Ochyromerina from Africa, with comments on the subtribe and description of immature stages (Coleoptera : Curculionidae : Curculioninae : Tychiini)

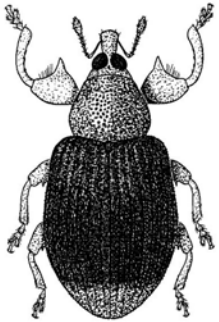
Rolf G. OBERPRIELER

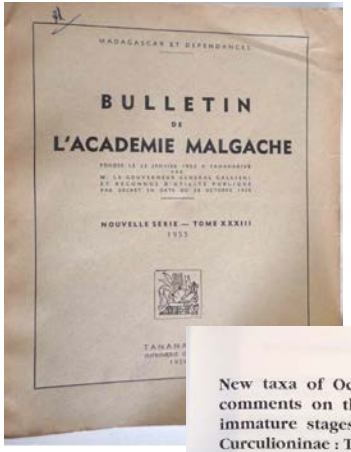
Voss 1937, Hustache 1956, Oberprieler 1993

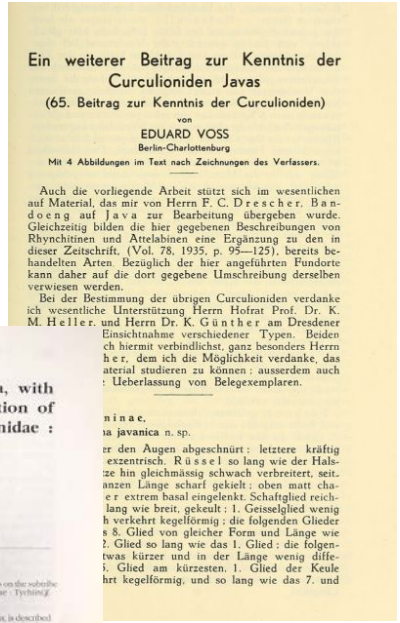
Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

Bibliographic synthesis





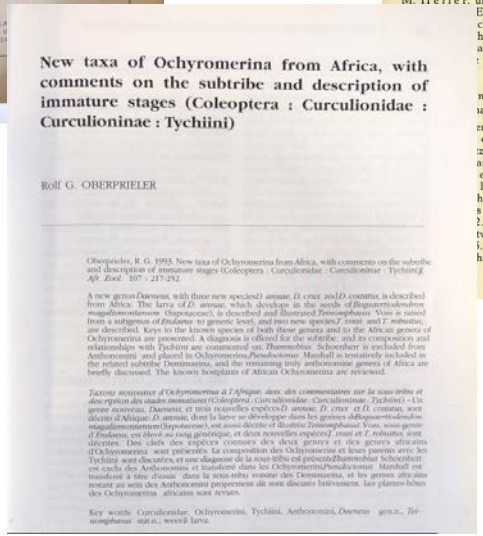



Ein weiterer Beitrag zur Kenntnis der Curculioniden Javas
(65. Beitrag zur Kenntnis der Curculioniden)
von
EDUARD VOSS
Berlin-Charlottenburg
Mit 4 Abbildungen im Text nach Zeichnungen des Verfassers.

Auch die vorliegende Arbeit stützt sich im wesentlichen auf Material, das mir von Herrn F. C. Drescher. Bandoeng auf Java zur Bearbeitung übergeben wurde. Gleichzeitig bilden die hier gegebenen Beschreibungen von Rhynchitinen und Attelabinen eine Ergänzung zu den in dieser Zeitschrift, (Vol. 78, 1935, p. 95—125), bereits behandelten Arten. Bezüglich der hier angeführten Fundorte kann daher auf die dort gegebene Umschreibung derselben verwiesen werden.

Bei der Bestimmung der übrigen Curculioniden verdanke ich wesentliche Unterstützung Herrn Hofrat Prof. Dr. K. M. Heller, und Herrn Dr. K. Günther am Dresdener Einsichtnahme verschiedener Typen. Beiden ich hiermit verbindlichst, ganz besonders Herrn her, dem ich die Möglichkeit verdanke, das aterial studieren zu können; ausserdem auch Ueberlassung von Belegexemplaren.

ninae,
a javanica n. sp.
er den Augen abgeschnürt: letztere kräftig exzentrisch. Rüssel so lang wie der Halsze hin gleichmässig schwach verbreitert, seitanzen Länge scharf gekielt; oben matt chaer extrem basal eingelenkt. Schaftglied reichlang wie breit, gekeult; 1. Geisselglied wenig verkehrt kegelförmig; die folgenden Glieder 8. Glied von gleicher Form und Länge wie 2. Glied so lang wie das 1. Glied; die folgentwas kürzer und in der Länge wenig diffe-. Glied am kürzesten. 1. Glied der Keule rt kegelförmig, und so lang wie das 7. und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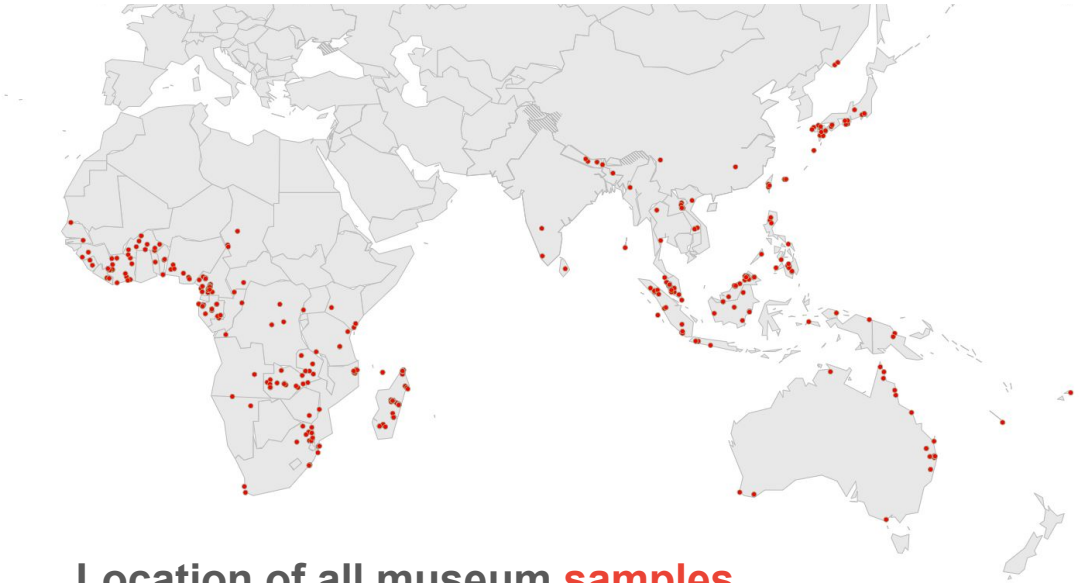
Voss 1937, Hustache 1956, Oberprieler 1993, Kojima 1997

Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

Complete survey of entomological collections



Location of all museum samples

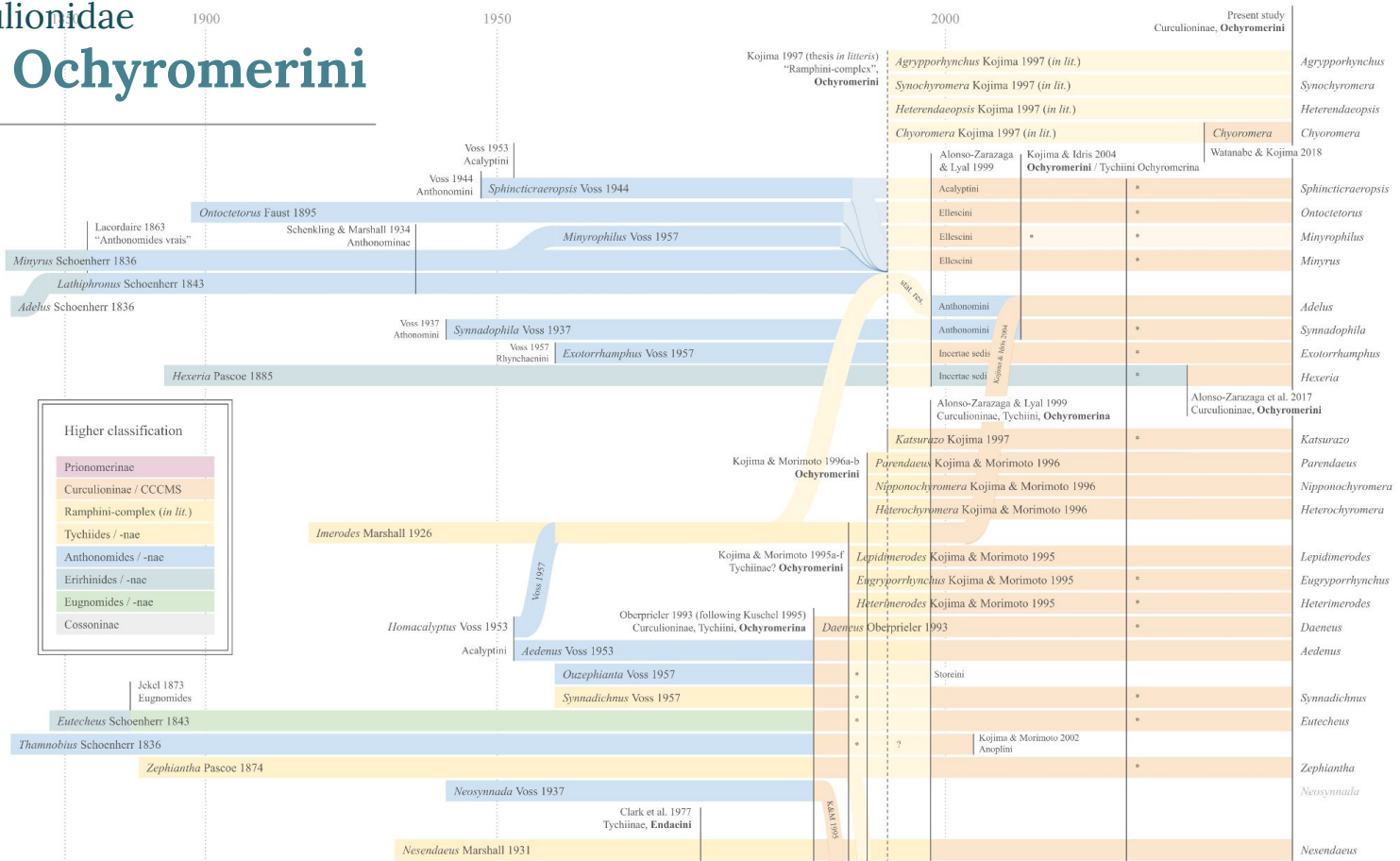
2740 specimens **identified** and **databased**

Order: Coleoptera

Family: Curculionidae

Tribe: **Ochyromerini**

Systematic review of all genera

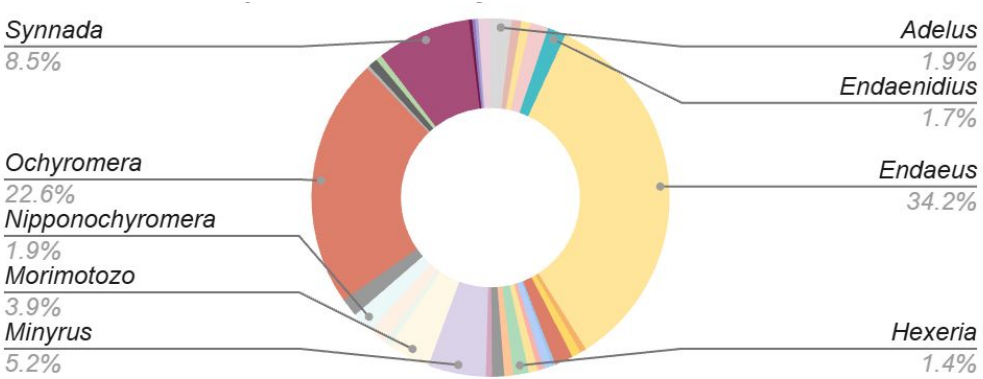


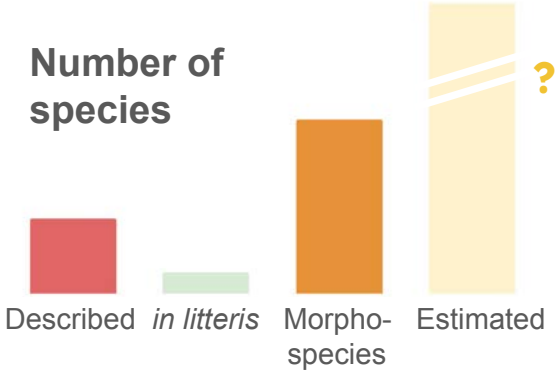
Order: Coleoptera
Family: Curculionidae

Tribe: **Ochyromerini**

2740 specimens identified

29 genera out of **37** described
85 species out of **258** described





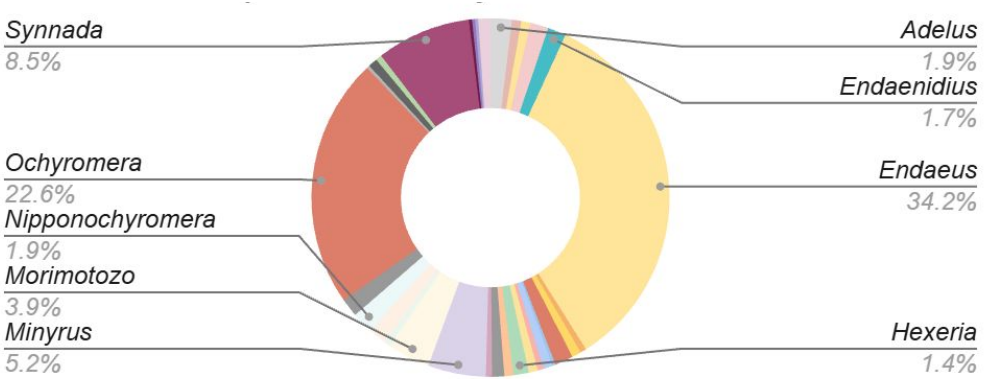
Order: Coleoptera
Family: Curculionidae

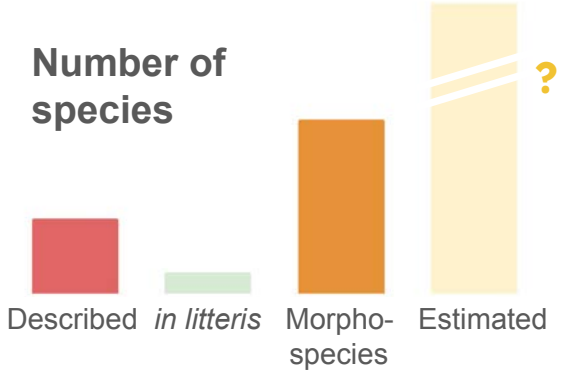
Tribe: **Ochyromerini**

2740 specimens identified

29 genera out of **37** described
85 species out of **258** described

>600 morphospecies identified!

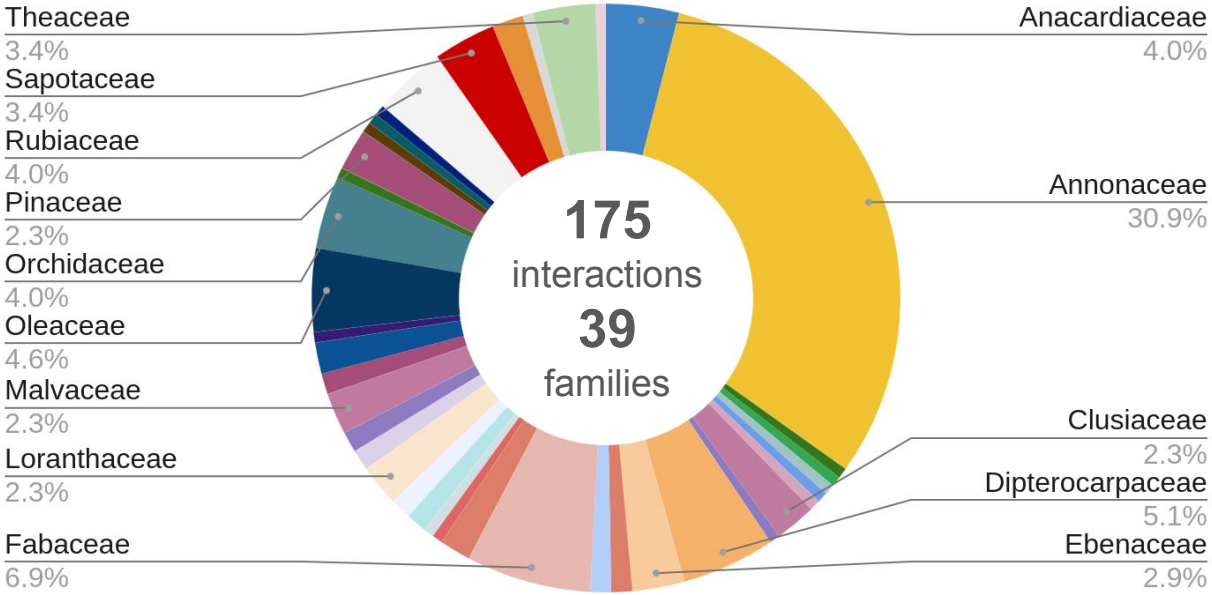




Order: Coleoptera

Family: Curculionidae

Tribe: **Ochyromerini**

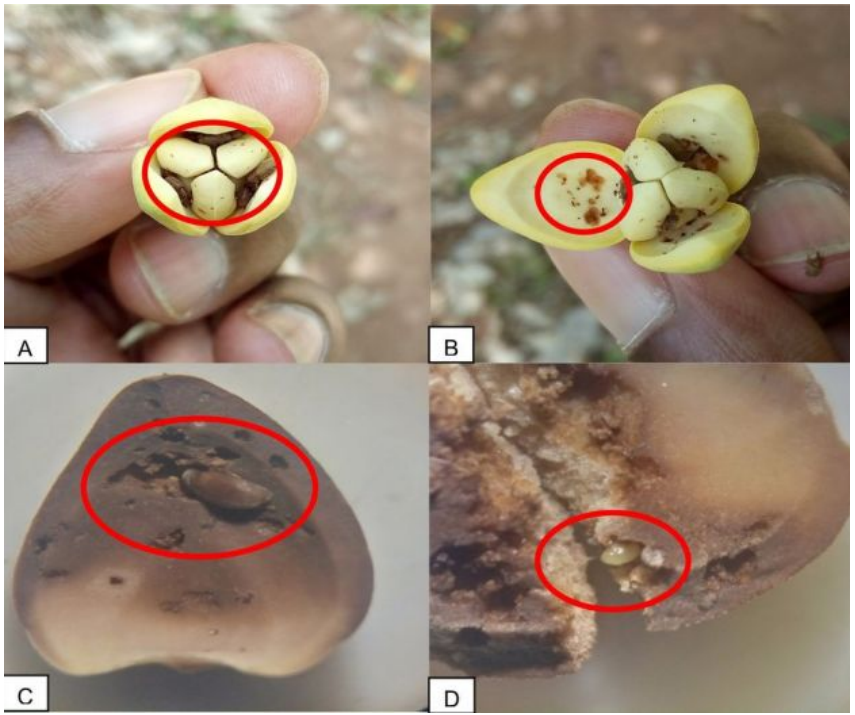


Annonaceae (*Annona*)

Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

Confirmed mutualism

Momose et al. 1998, Ratnayake et al. 2006, 2007, Lau et al. 2016, 2017, Watanabe et al. 2017, Saunders 2020, Dao et al. 2023…



Annona senegalensis (**Annonaceae**), *Endaeus floralis* & *E. castus*

Dao et al. 2023

Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

Confirmed mutualism

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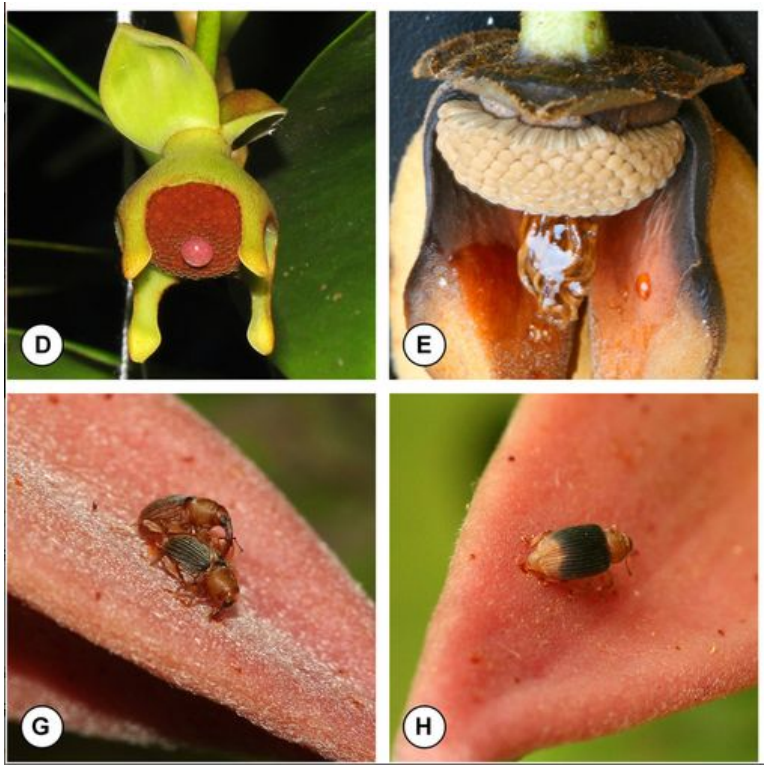


Saunders 2020

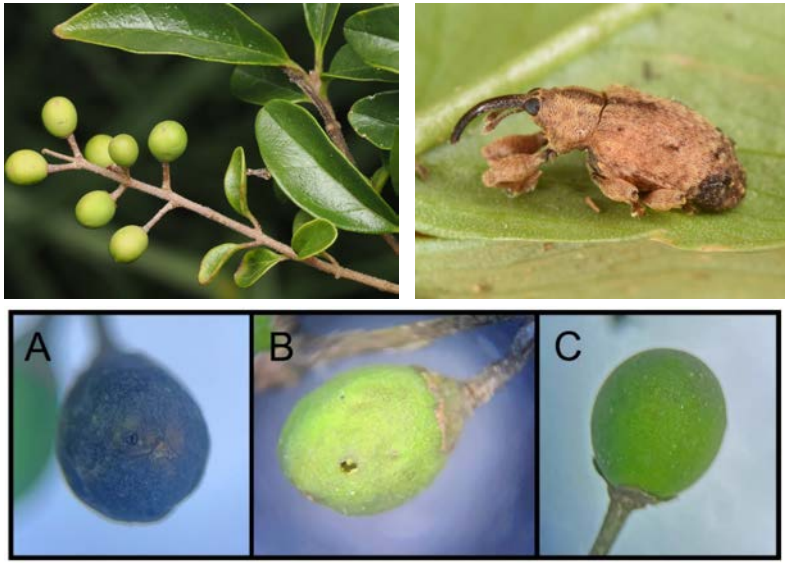
Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

Confirmed mutualism

Momose et al. 1998, Ratnayake et al. 2006, 2007, Lau et al. 2016, 2017, Watanabe et al. 2017, Saunders 2020, Dao et al. 2023…

Confirmed antagonism

Marshall 1926b, Miwa 1940, Wray 1961, Kojima et Morimoto 1996a, Tokuda et al. 2000, Kojima 2011a-b, Kallekkattil et al. 2020, Hsiao et al. 2025…



Ligustrum spp. (Oleaceae), *Ochyromera ligustri*

Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

Confirmed mutualism

Momose et al. 1998, Ratnayake et al. 2006, 2007, Lau et al. 2016, 2017, Watanabe et al. 2017, Saunders 2020, Dao et al. 2023…

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@harumkoh

Abies spp. (Pinaceae), *Parendaeus abietinus*

Order: Coleoptera
Family: Curculionidae
Tribe: **Ochyromerini**

Confirmed mutualism

Momose et al. 1998, Ratnayake et al. 2006, 2007, Lau et al. 2016, 2017, Watanabe et al. 2017, Saunders 2020, Dao et al. 2023…

Confirmed antagonism

Marshall 1926b, Miwa 1940, Wray 1961, Kojima et Morimoto 1996a, Tokuda et al. 2000, Kojima 2011a-b, Kallekkattil et al. 2020, Hsiao et al. 2025…

Probable mutualism

Probable antagonism

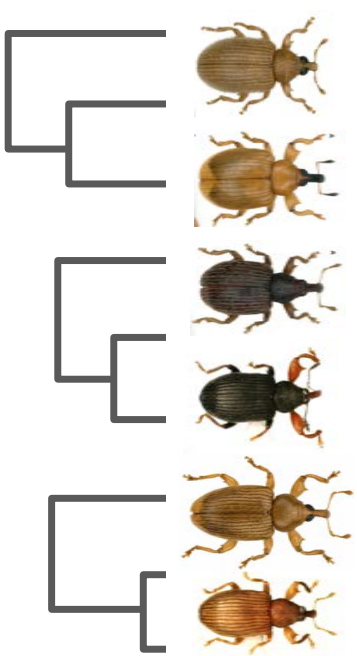
- Niche conservatism of closely related species
- Naturalist expertise (convergent traits, larval habits, adult behavior)

Evolutionary hypotheses

Evolutionary hypotheses

- ☐ Monophyly of Ochyromerini

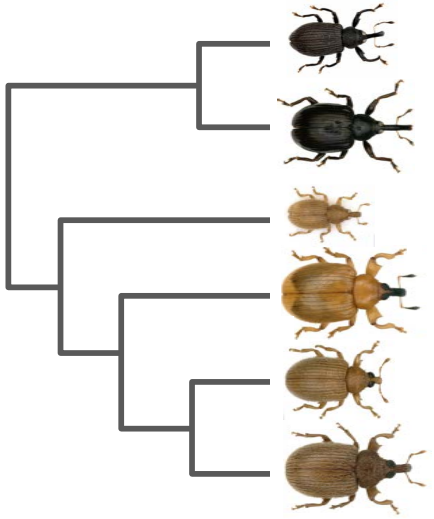
Evolutionary hypotheses



Host plants

- ☐ Monophyly of Ochyromerini
- ☐ Niche conservatism of host plant families

Evolutionary hypotheses



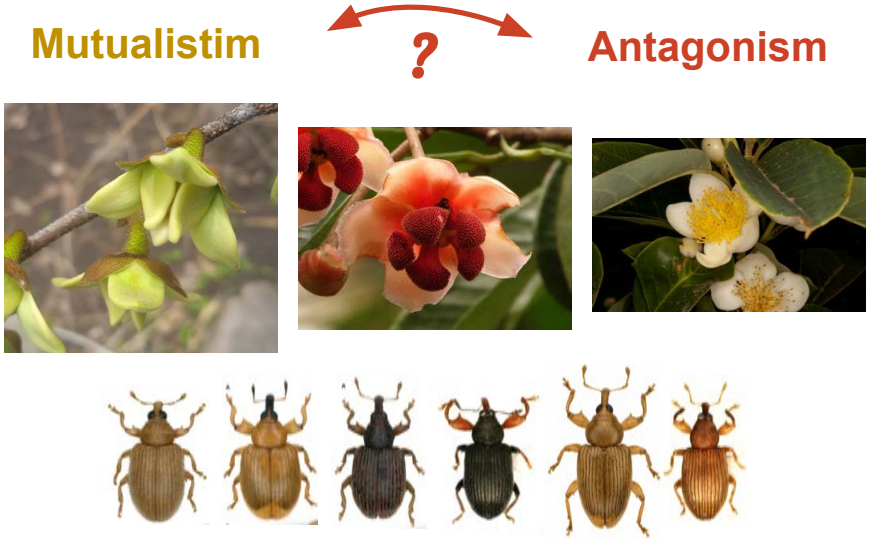
Antagonists

Mutualists

- ☐ Monophyly of Ochyromerini
- ☐ Niche conservatism of host plant families
- ☐ Monophyly of pollinating Ochyromerini

Objectives

Reconstruct the **evolutionary history of Ochyromerini**
to better **understand the emergence of mutualism in this tribe**
and ultimately **the evolution of brood-site pollination** in the tropics



Material and Methods

Taxon sampling

2740 specimens

Sub-sampled to **540 specimens** representing the Ochyromerini diversity

- **29** Ochyromerini **genera**
- **348 species** and morphospecies
- **31** outgroups

Taxon sampling

2740 specimens

Sub-sampled to **540 specimens** representing the Ochyromerini diversity

- **29** Ochyromerini **genera**
- **348 species** and morphospecies
- **31** outgroups

>700 specimens dissected and mounted back for museum collections

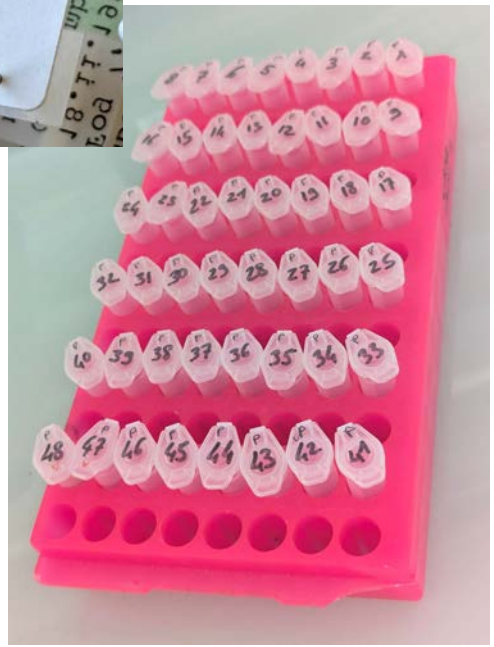
DNA extraction

- **Non-destructive DNA extraction**

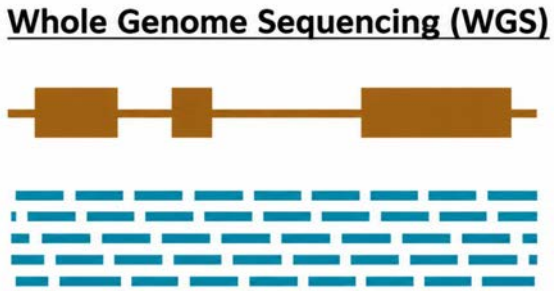
EZ-10 Spin Column Animal Genomic DNA Miniprep Kit (BioBasic)

- Fine-tuned protocol for **degraded** and **quantitatively sparse DNA** (<1ng/µL)

Santa Cruz Reaction (SCR; 42 specimens; Kapp et al. 2021)
NEBNext Ultra II DNA Library Prep Kit for Illumina (New England BioLabs)



Library construction: WGS and Target capture

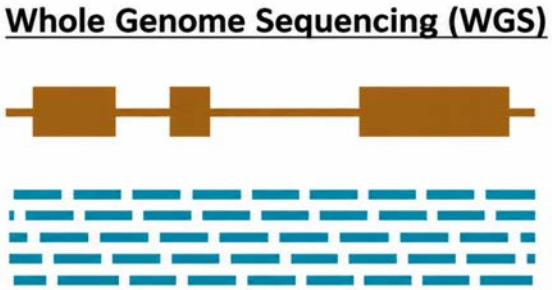


- Whole genome with low coverage

“Fresh” samples with better DNA quality

Gorcenco et al. 2020

Library construction: WGS and Target capture



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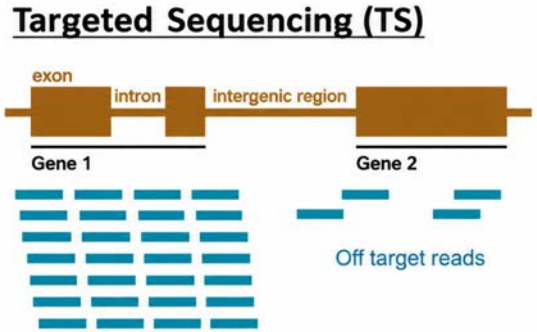
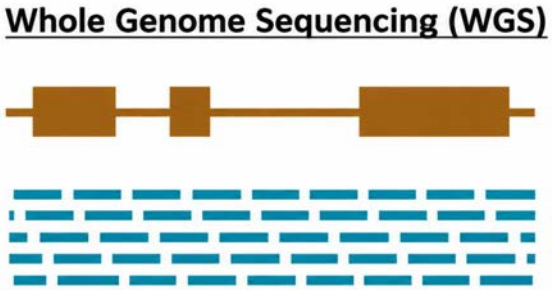


- Thousands of targeted genomic regions

Numerous museum samples with more or less degraded DNA

Gorcenco et al. 2020

Library construction: WGS and Target capture



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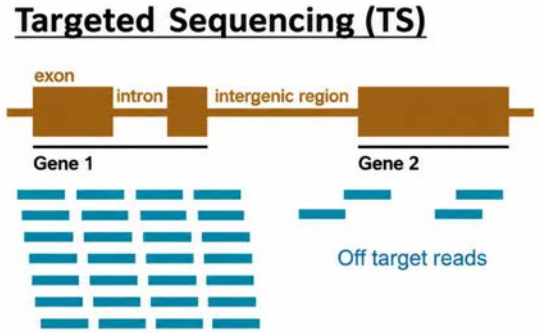
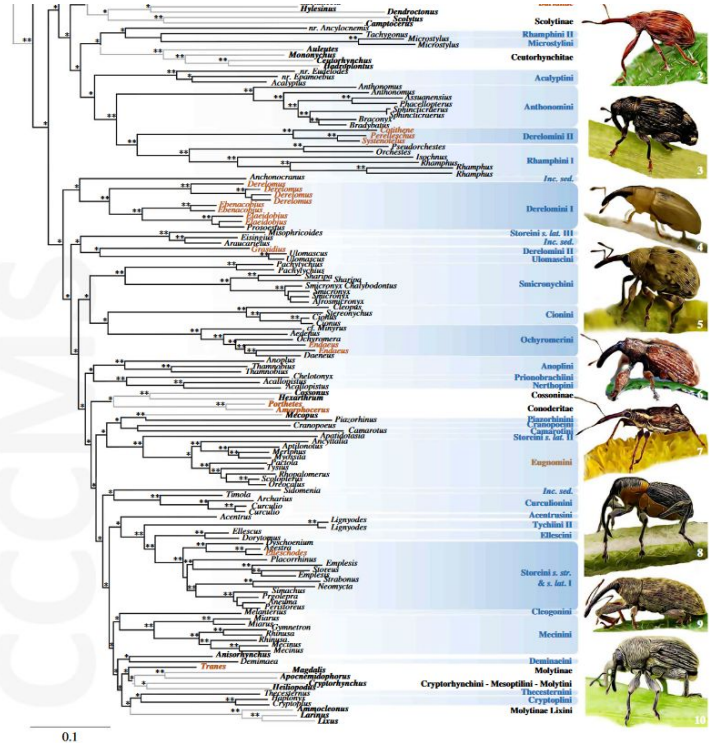


- Thousands of **targeted genomic regions?**

Numerous museum samples with more or less degraded DNA

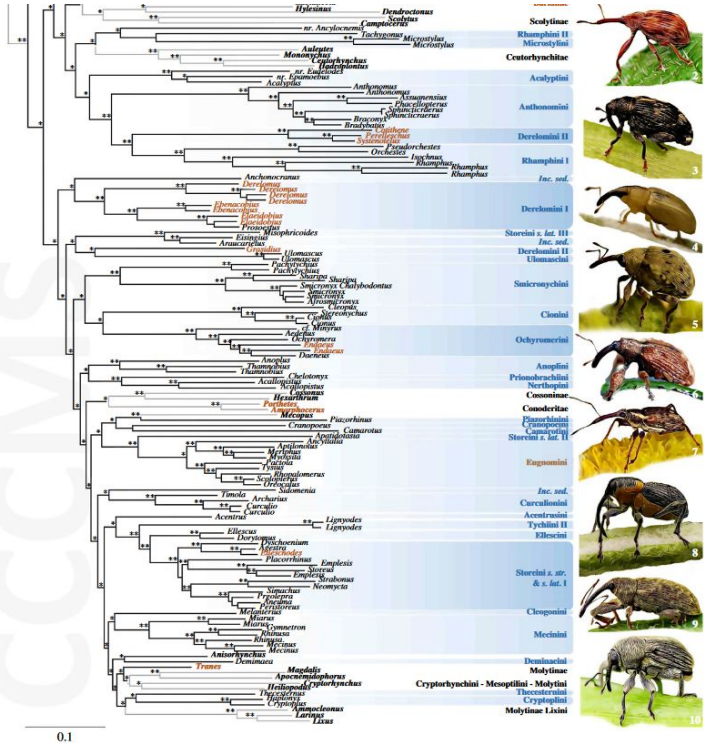
Gorcenco et al. 2020

Target capture markers for weevils



Haddad et al. 2018, Shin et al. 2018, Li et al. 2023, Haran et al. 2023b

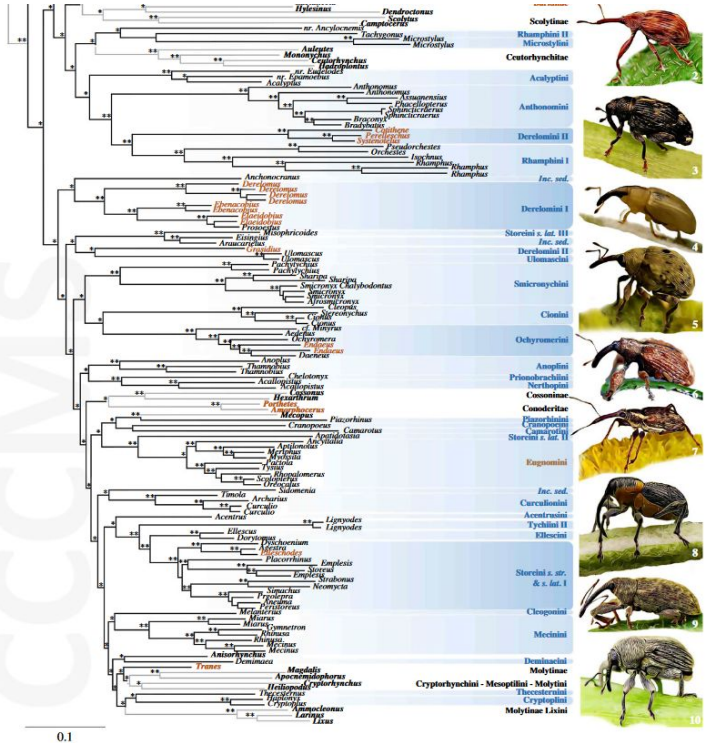
Target capture markers for weevils



- Genomic markers designed for **Coleoptera** (400k spp.) with only 7 reference genomes
- Too conserved, not enough **phylogenetic resolution**
- **Quantitatively insufficiant** to cope with data loss and filtrations

Haddad et al. 2018, Shin et al. 2018, Li et al. 2023, Haran et al. 2023b

Target capture markers for weevils



- Genomic markers designed for **Coleoptera** (400k spp.) with only 7 reference genomes
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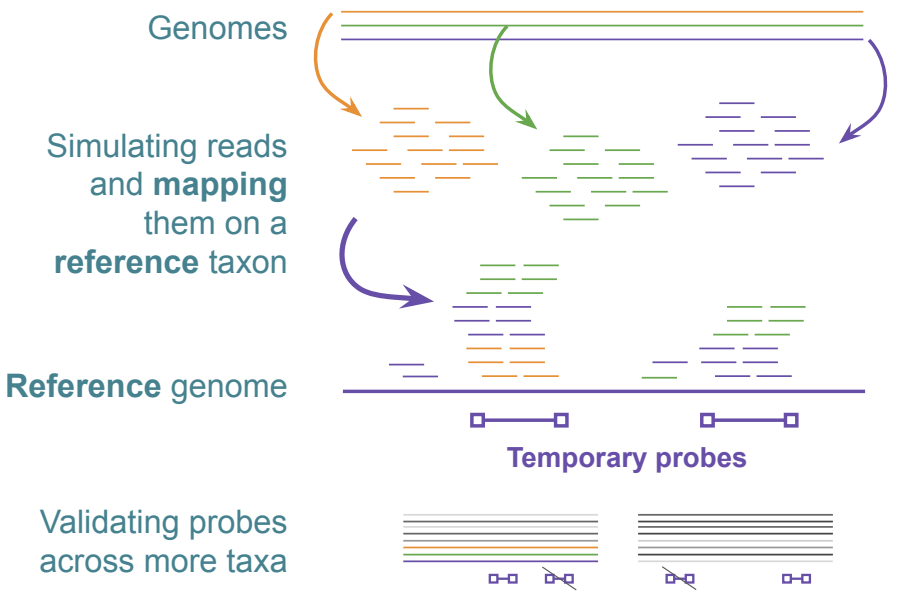
We need a new set of more numerous and adapted markers specifically designed for weevils

Haddad et al. 2018, Shin et al. 2018, Li et al. 2023, Haran et al. 2023b

Current method to identify target capture markers: PHYLUCE

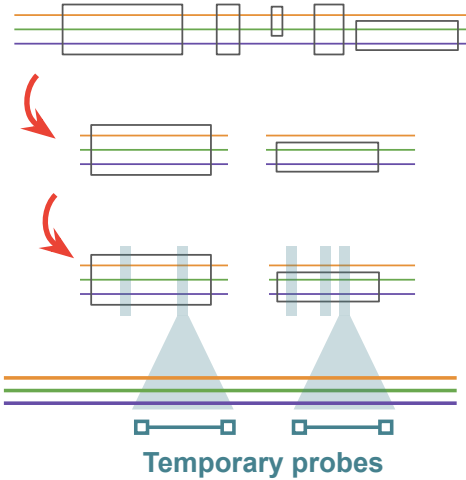


- Identifies ultraconserved elements (**UCE**) that still lack phylogenetic resolution
- Strong bias due to the **single genomic reference**

Faircloth 2016

- Genome Alignment-based Bait Inference (GABBI)
- No **single genomic reference** thanks to the genome alignment
- Targeted region identification is **less constrained** than a stringent read mapping procedure

New method I developed during this thesis: GABBI



Genome alignment
ProgressiveCactus

MAFfilter

Identify **shared** and **homologous regions**
PhastCons

Validating probes across more taxa

Enriching the probe set with **ancestral sequences**

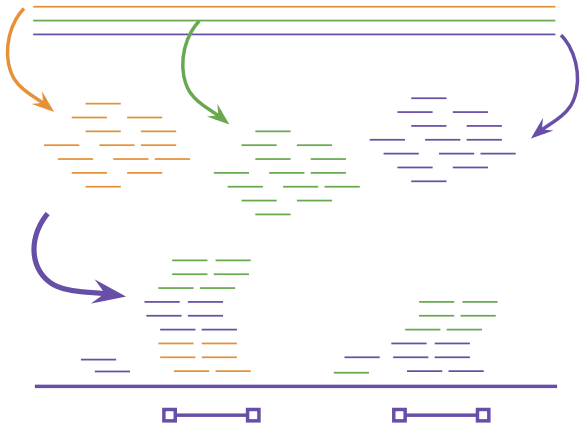
Zelvelder et al. 2026 (preprint)

Current method to identify target capture markers: PHYLUCE

Genomes

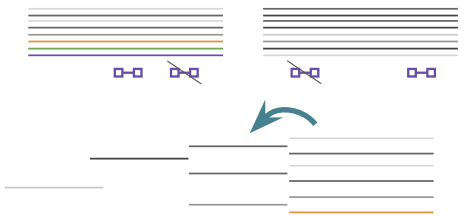
Simulating reads and **mapping** them on a **reference** taxon

Reference genome

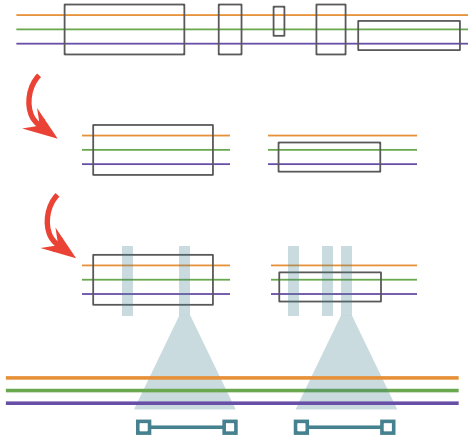


Validating probes across more taxa

Enriched with **ancestral sequences**



New method I developed during this thesis: GABBI



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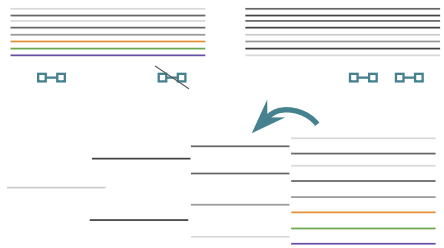
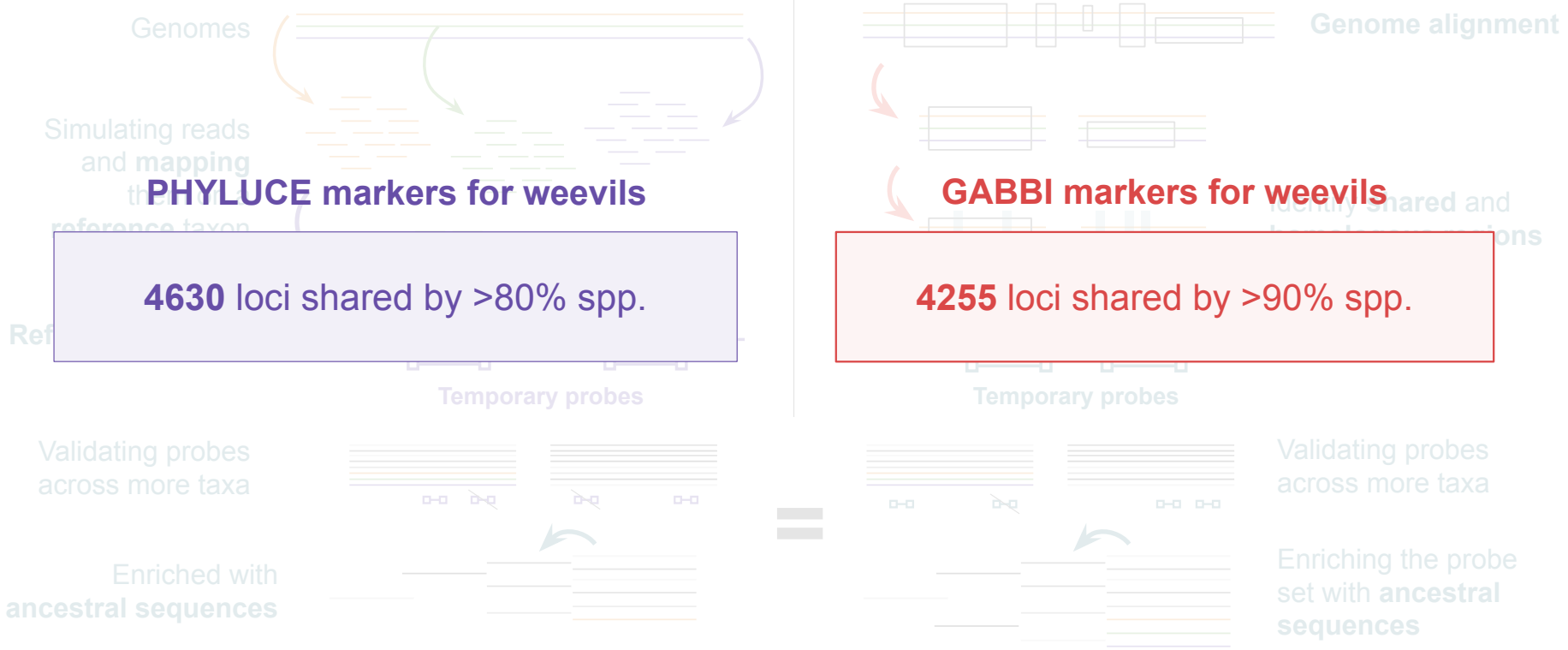


Current method to identify target capture markers: PHYLUCE

New method I developed during this thesis: GABBI



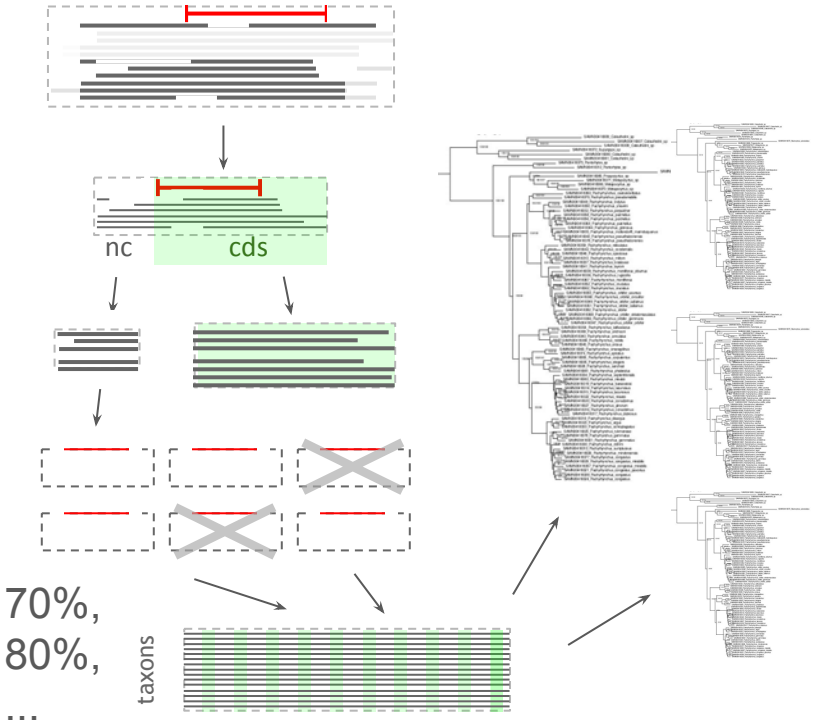
PHYLUCE markers for weevils

4630 loci shared by >80% spp.

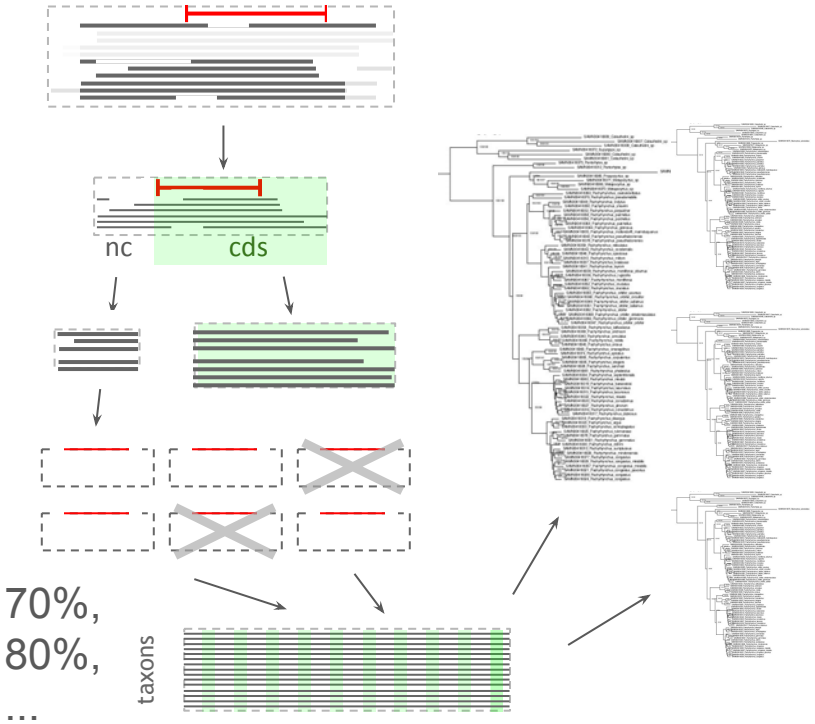
GABBI markers for weevils

4255 loci shared by >90% spp.

Phylogenomic analyses



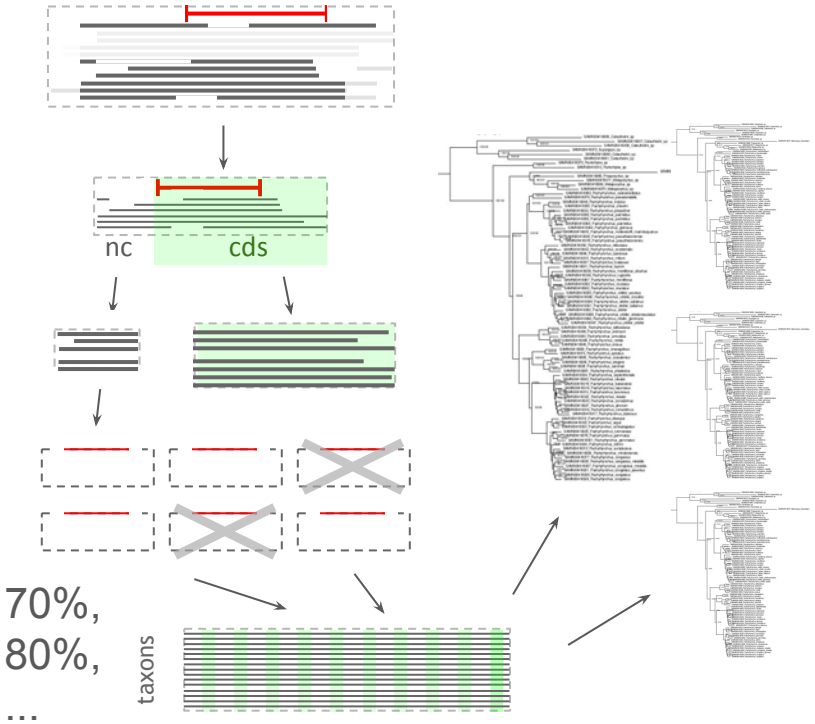
Phylogenomic analyses



- **Assembling** reads

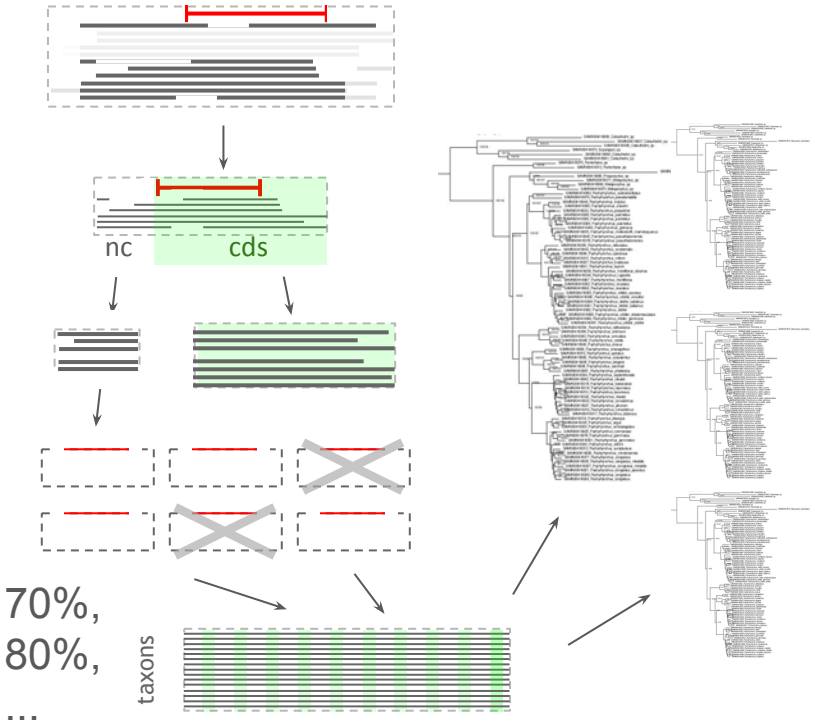
  aTRAM, SPADES, BLAST

Phylogenomic analyses



- **Assembling** reads
  aTRAM, SPADES, BLAST
- **Filtering** contaminations by detecting clusters of sequences
  Custom R script using ape and igraph

Phylogenomic analyses



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- **Filtering** contaminations by detecting clusters of sequences
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  MAFFT

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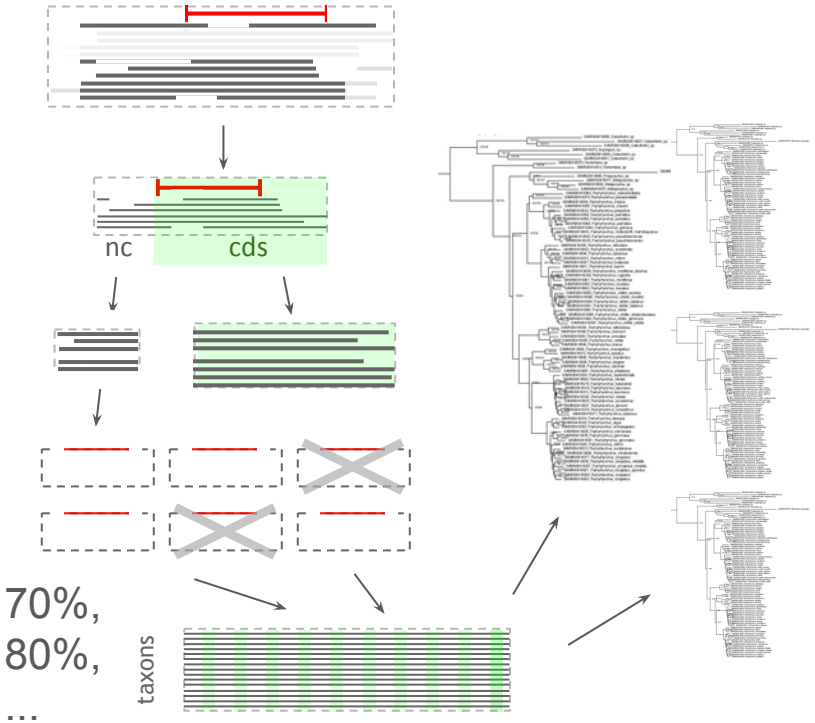

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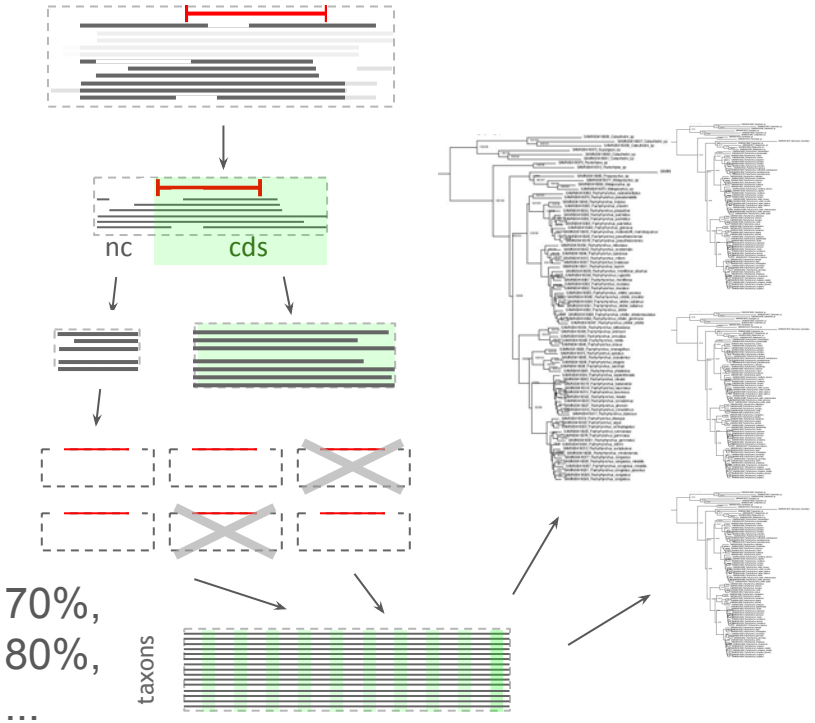

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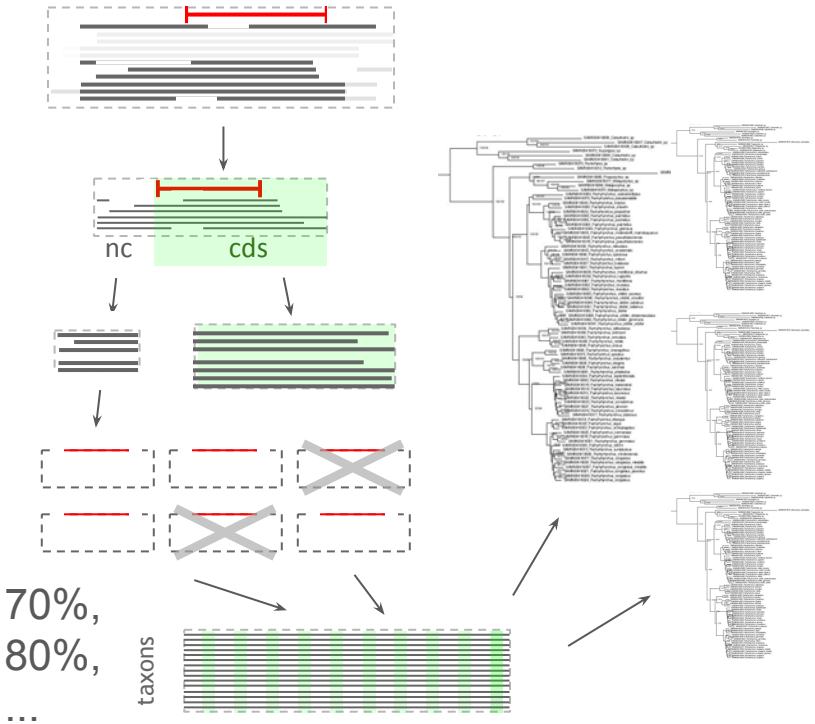

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- **Building** the character matrix (supermatrix)
  AMAS
- **Phylogenetic inferences** of gene trees and species trees
  IQTREE, ASTRALw, CASTER, Phylobayes

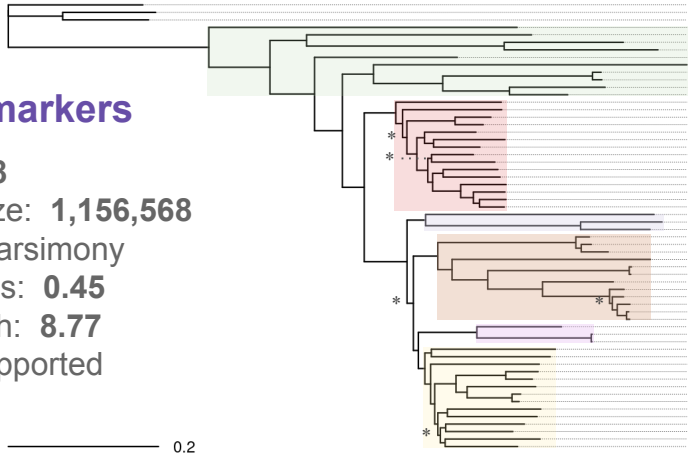
Results

Maximum likelihood framework with MFP+MERGE model

Curculionoidea superfamily
70% spp.

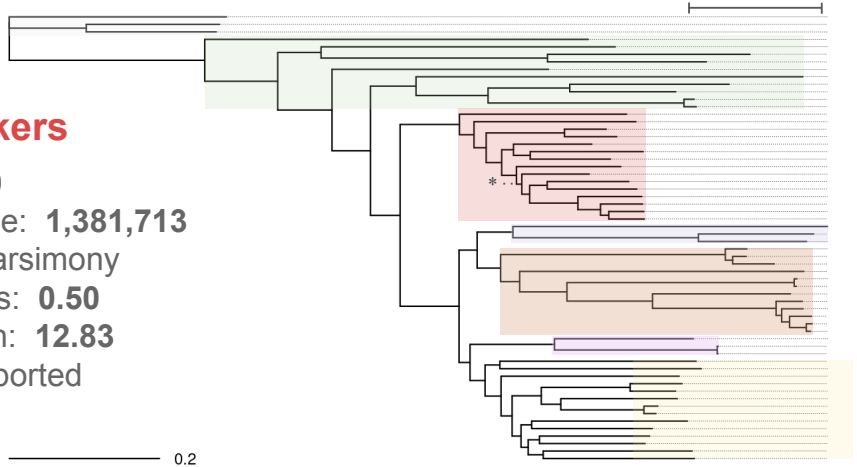
PHYLUCE markers

Markers: **3,568**
Supermatrix size: **1,156,568**
Proportion of parsimony informative sites: **0.45**
Total tree length: **8.77**
5 nodes not supported



GABBI markers

Markers: **3,239**
Supermatrix size: **1,381,713**
Proportion of parsimony informative sites: **0.50**
Total tree length: **12.83**
1 node not supported



Anthribidae

'Early diverging lineages'

CEGH

Curculioninae II

Scolytinae

Ceutorhynchinae

Curculioninae I + Molytinae

Zelvelder et al. 2026 (preprint)

Maximum likelihood framework with MFP+MERGE model

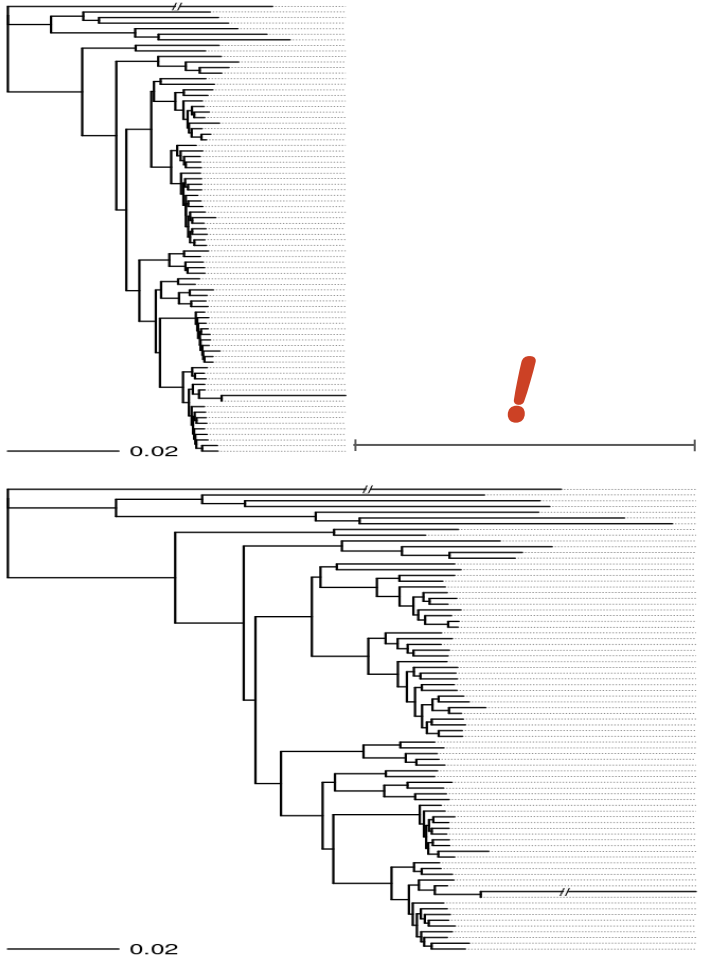
Pachyrhynchini tribe
70% spp.

PHYLUCE markers

Markers: **1,335**
Supermatrix size: **266,716**
Proportion of parsimony informative sites: **0.10**
Total tree length: **0.65**
21 nodes not supported

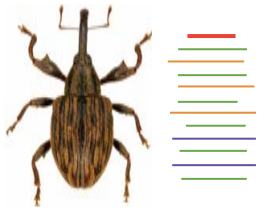
GABBI markers

Markers: **1,161**
Supermatrix size: **261,147**
Proportion of parsimony informative sites: **0.20**
Total tree length: **1.51**
14 nodes not supported



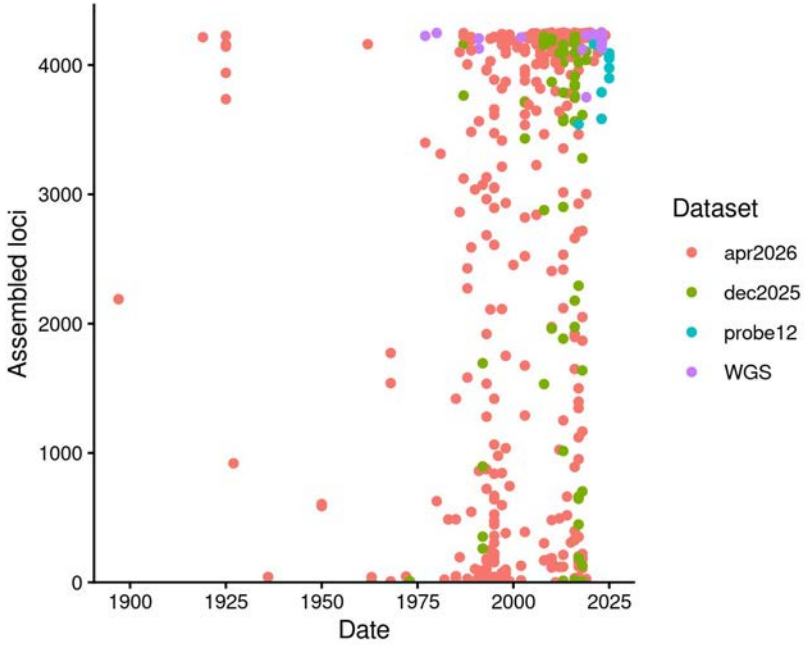
data from Van Dam et al. 2023, Syst. Bio.

Target capture results



New set of **shared homologous regions (SHR)** for target enrichment of **weevils** (Coleoptera, Curculionoidea)

Target capture results



- Median of 3 827 loci assembled in our **460 museum samples** = **90%** of all markers !
  (WGS reach 95% of all markers assembled)

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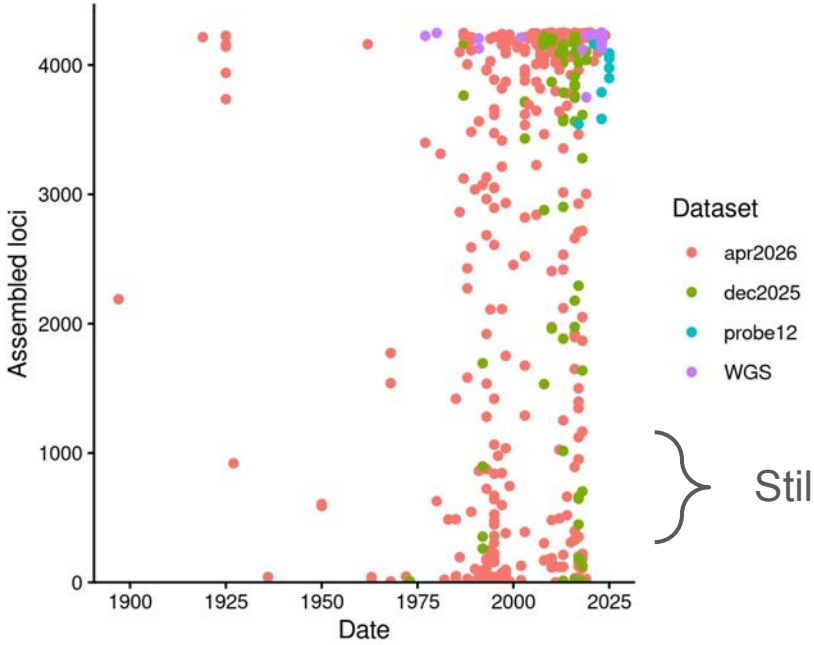

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Still hundreds of markers in specimens that “failed”!

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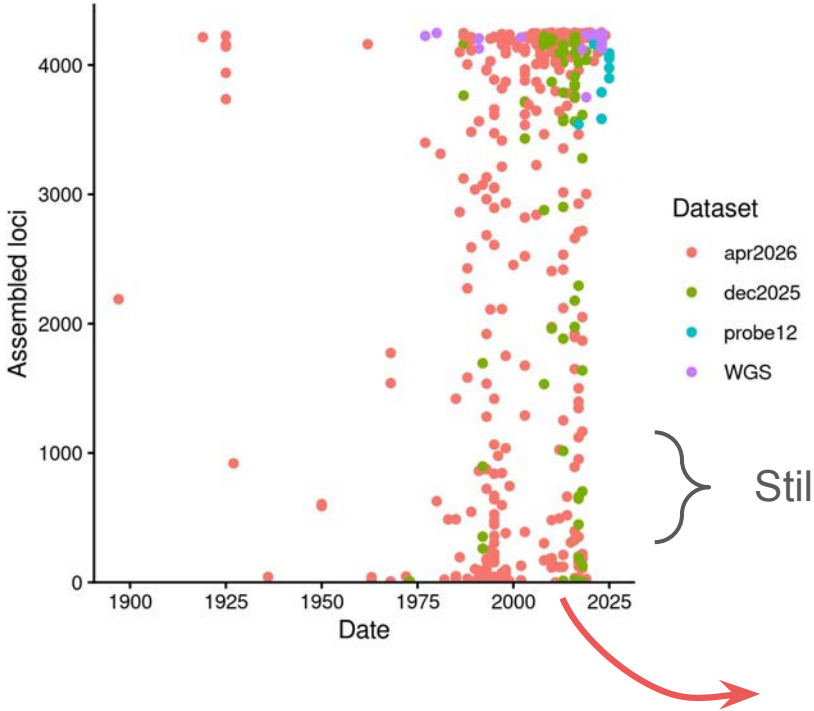

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Degraded DNA in recent specimens

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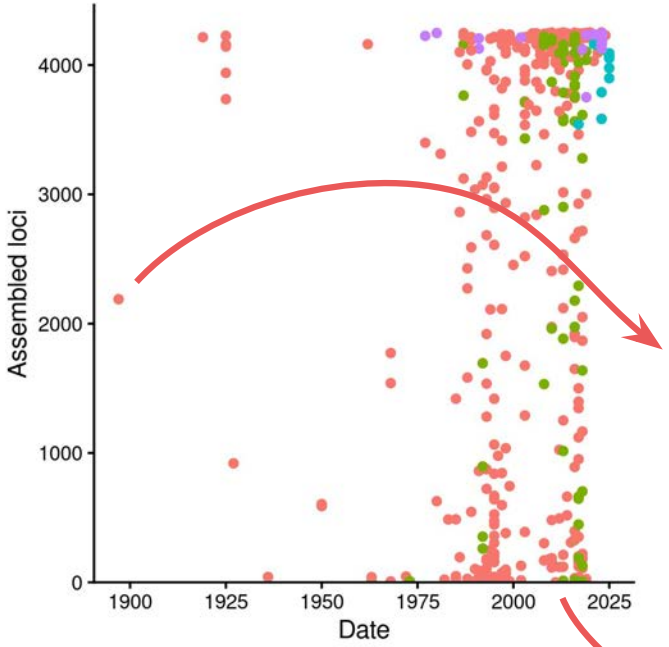

!

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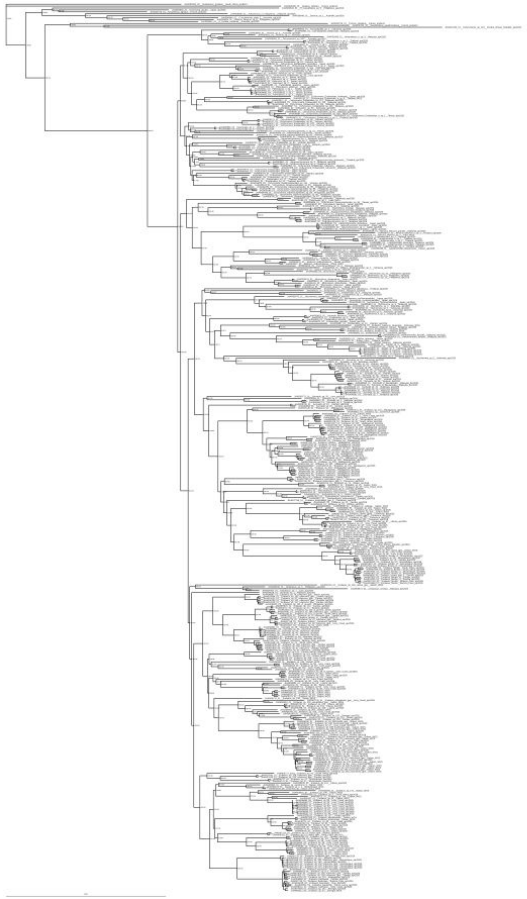
Type species *Eusynnada plaxoides*
MNHN, 1897
(129 years old)

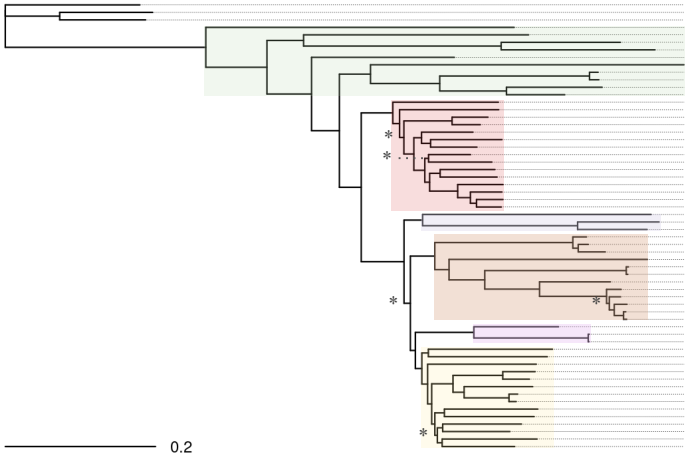
Degraded DNA in recent specimens

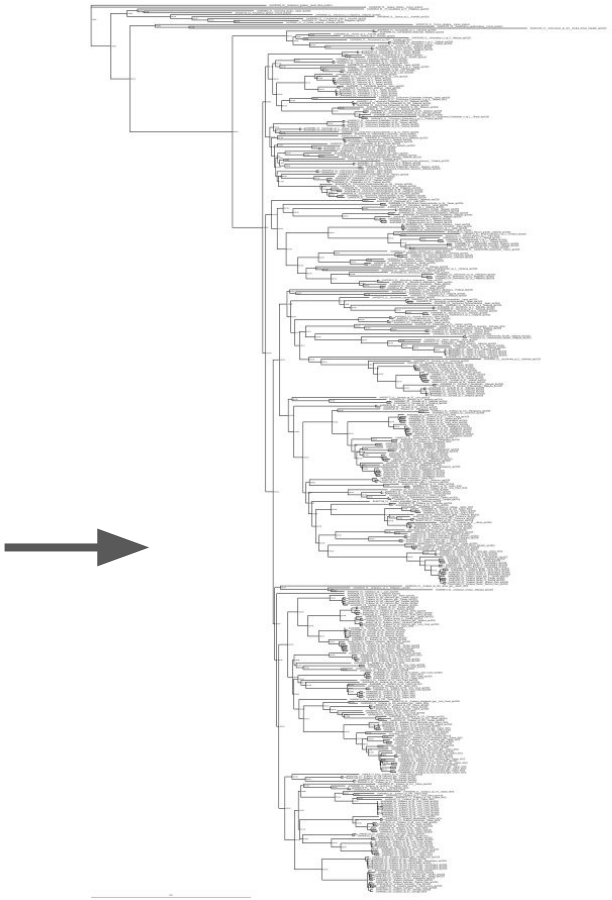
Phylogenetic inferences



Phylogenetic inferences

Few days





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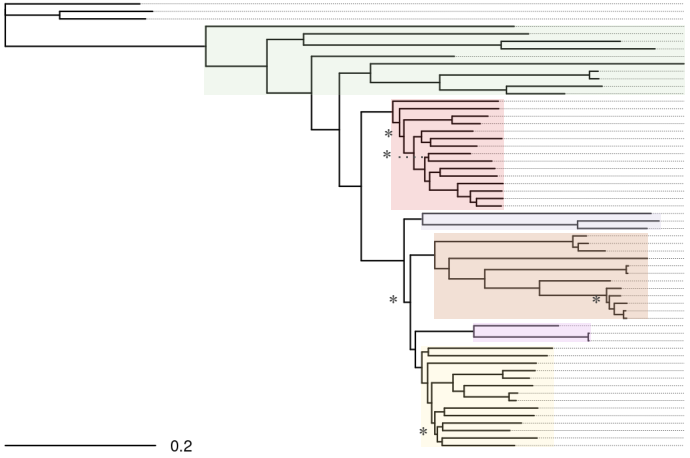

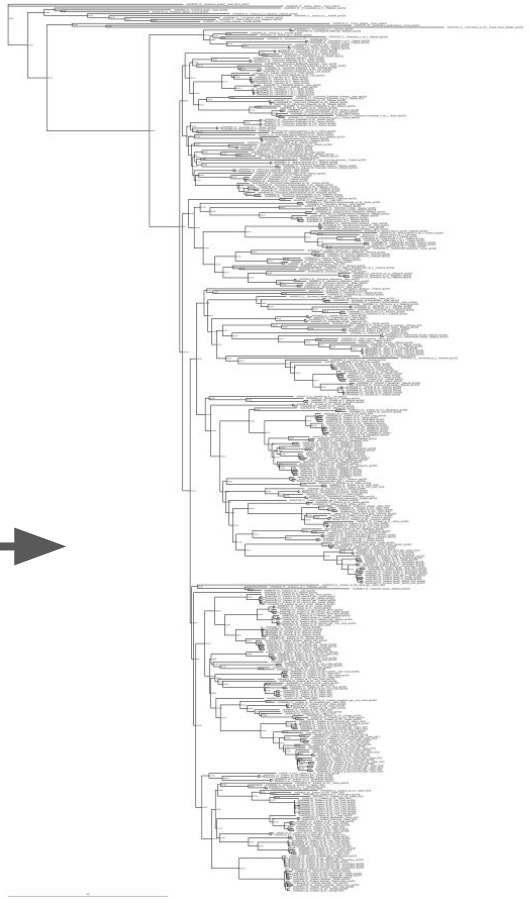

Few months!

Phylogenetic inferences

- **Quicker** but more **approximatives** analyses on the entire sample
  CASTER-site, CASTER-pair, wASTRAL

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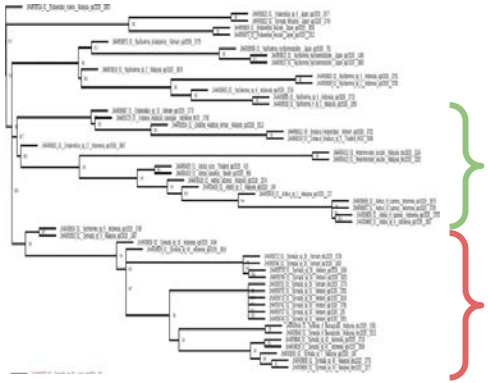
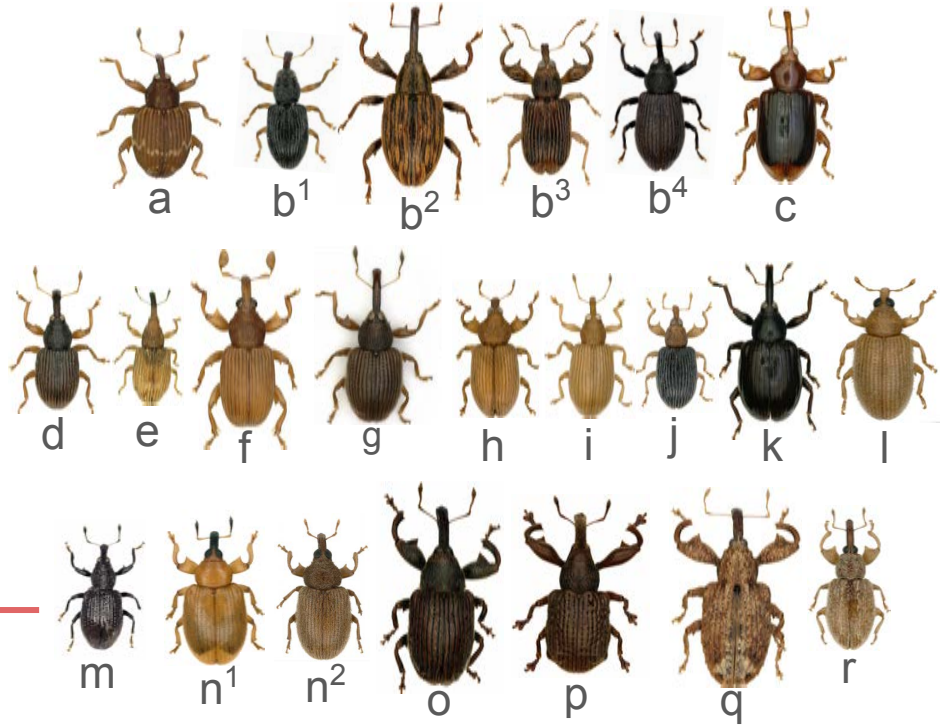
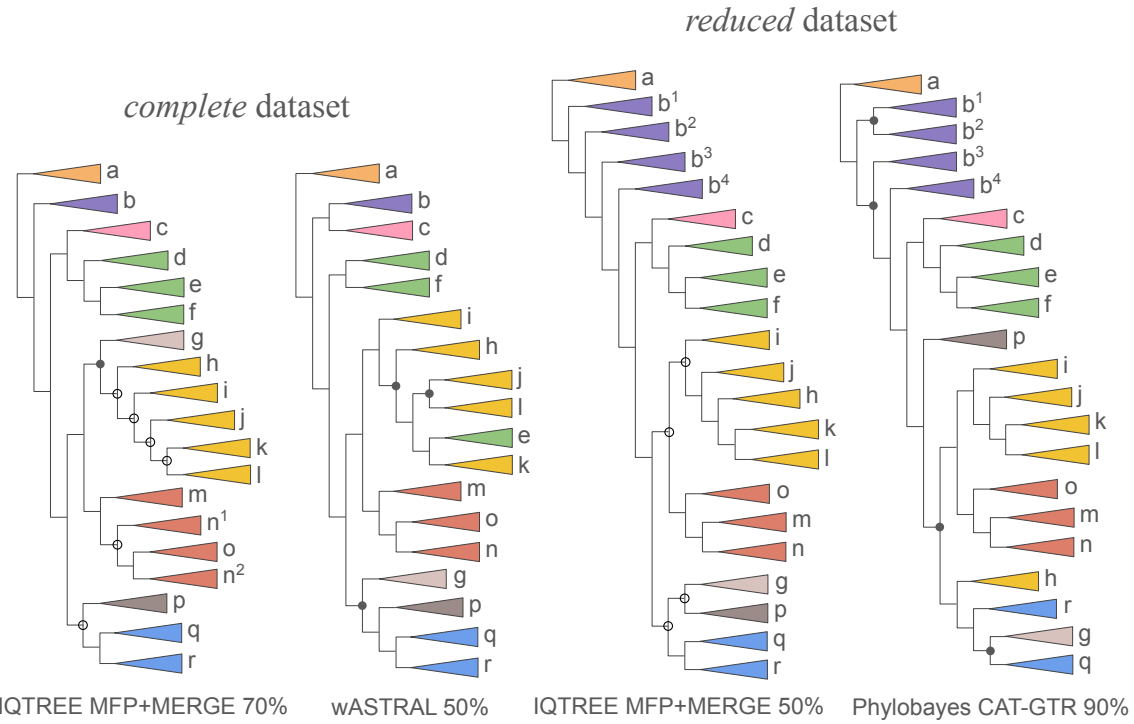
  ↳ Defining ‘stable’ **clades**





Phylogenetic inferences

- **More thorough** analyses on the *reduced* dataset and the *complete* dataset
  IQTREE avec MFP+MERGE, wASTRAL, Phylobayes



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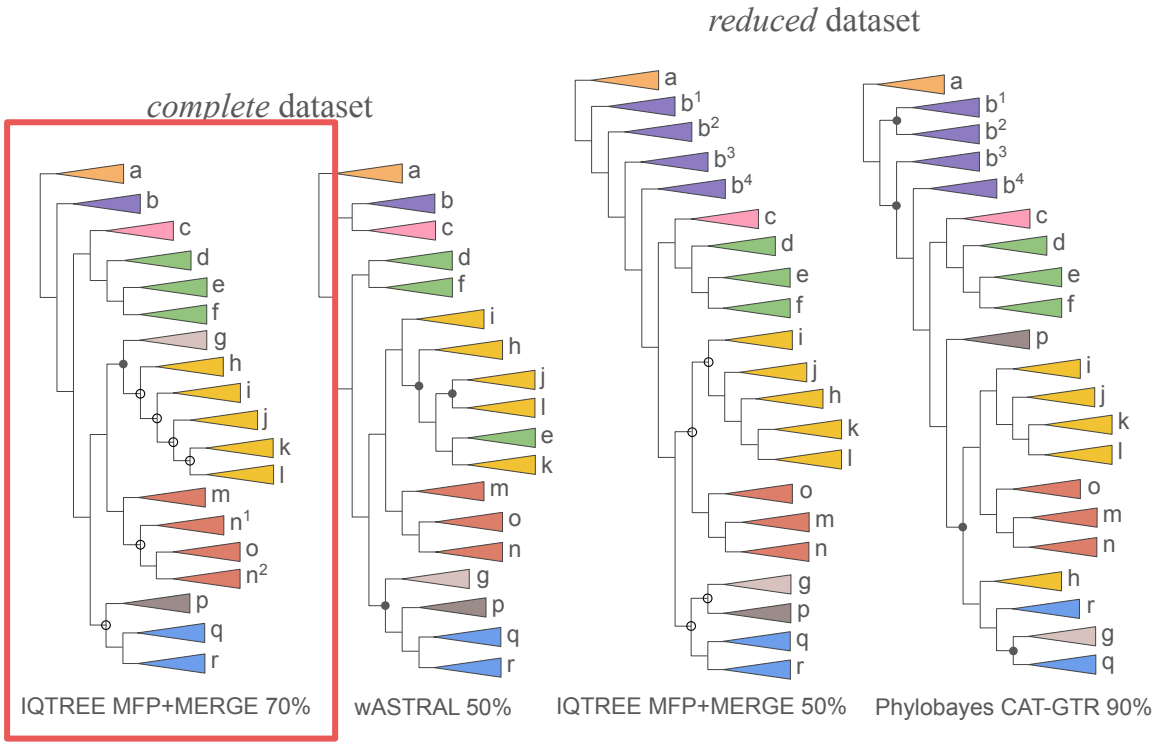

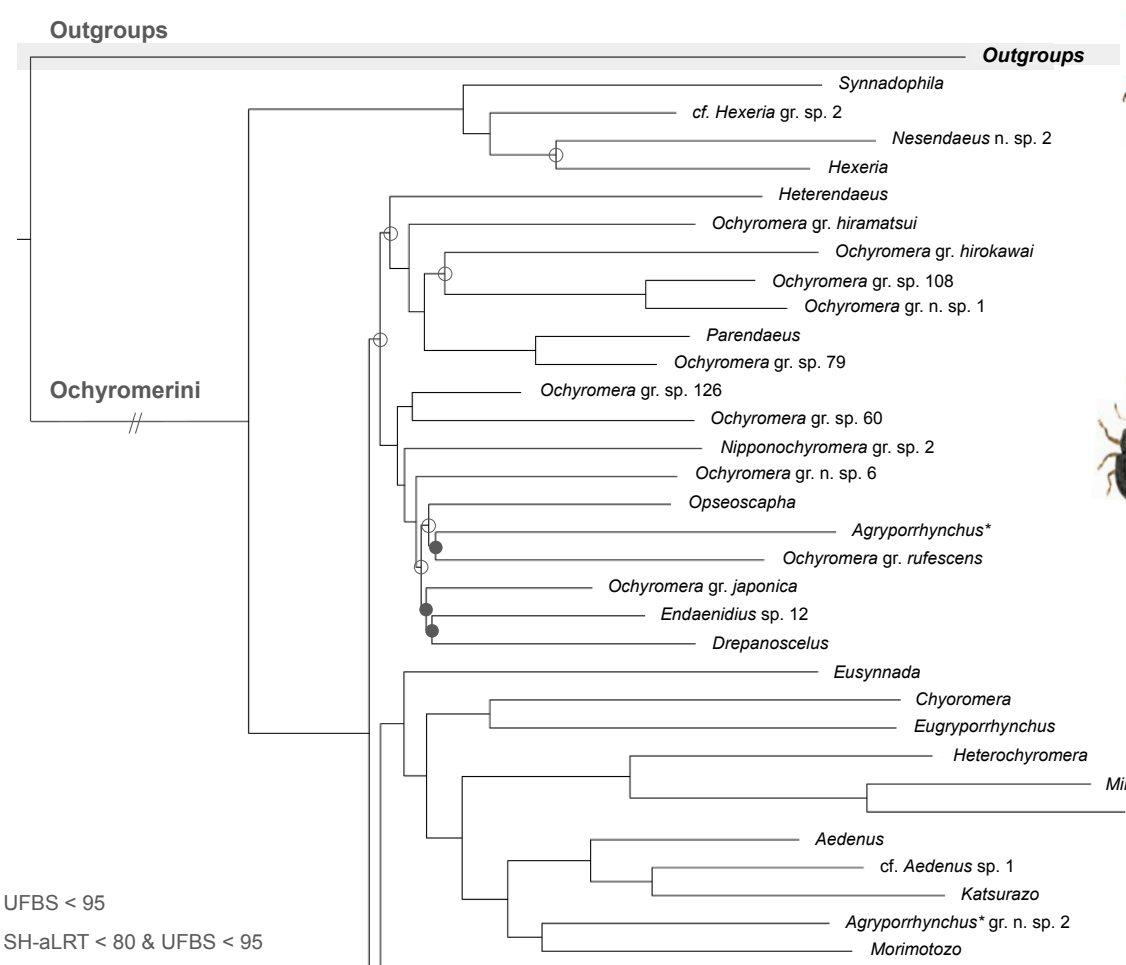
Outgroups
Outgroups
Synnadophila
cf. Hexeria gr. sp. 2
Nesendaeus n. sp. 2
Hexeria
Heterendaeus
Ochyromera gr. hiramatsui
Ochyromera gr. hirokawai
Ochyromera gr. sp. 108
Ochyromera gr. n. sp. 1
Parendaeus
Ochyromera gr. sp. 79
Ochyromerini
Ochyromera gr. sp. 126
Ochyromera gr. sp. 60
Nipponochyromera gr. sp. 2
Ochyromera gr. n. sp. 6
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Agryporrhynchus*
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UFBS < 95
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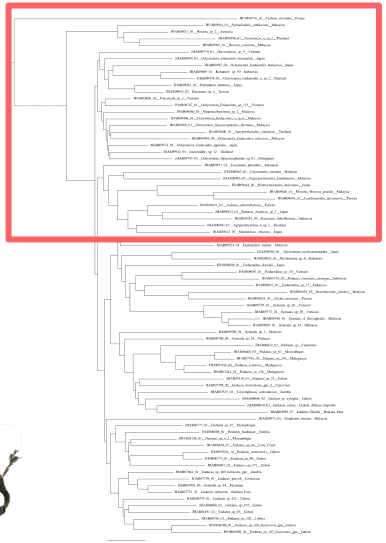

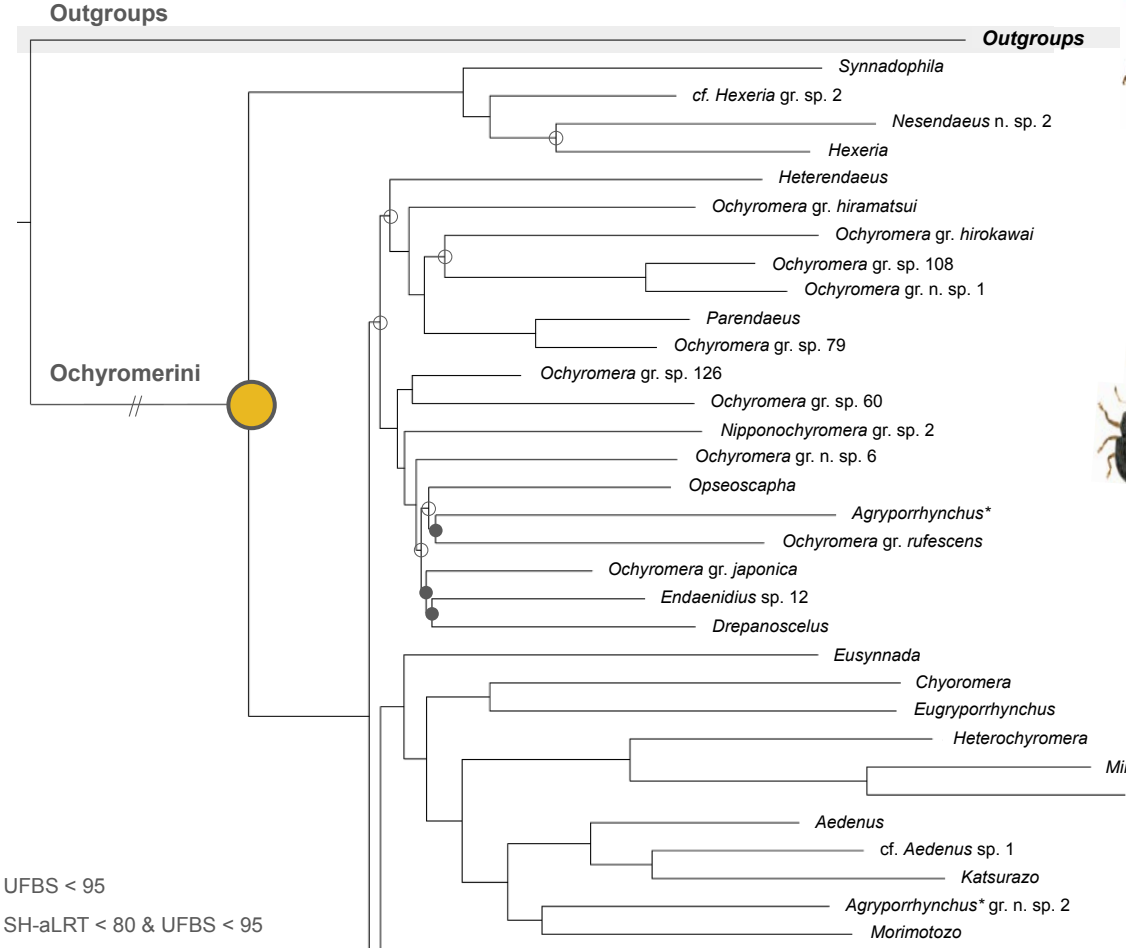
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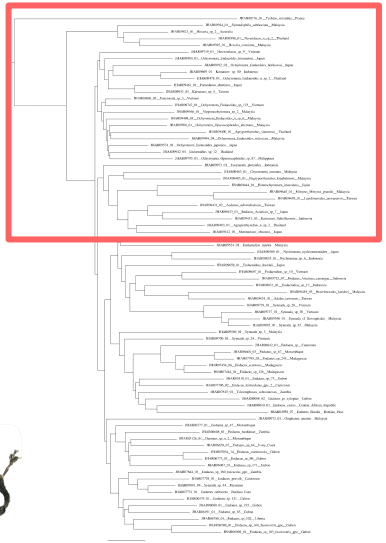

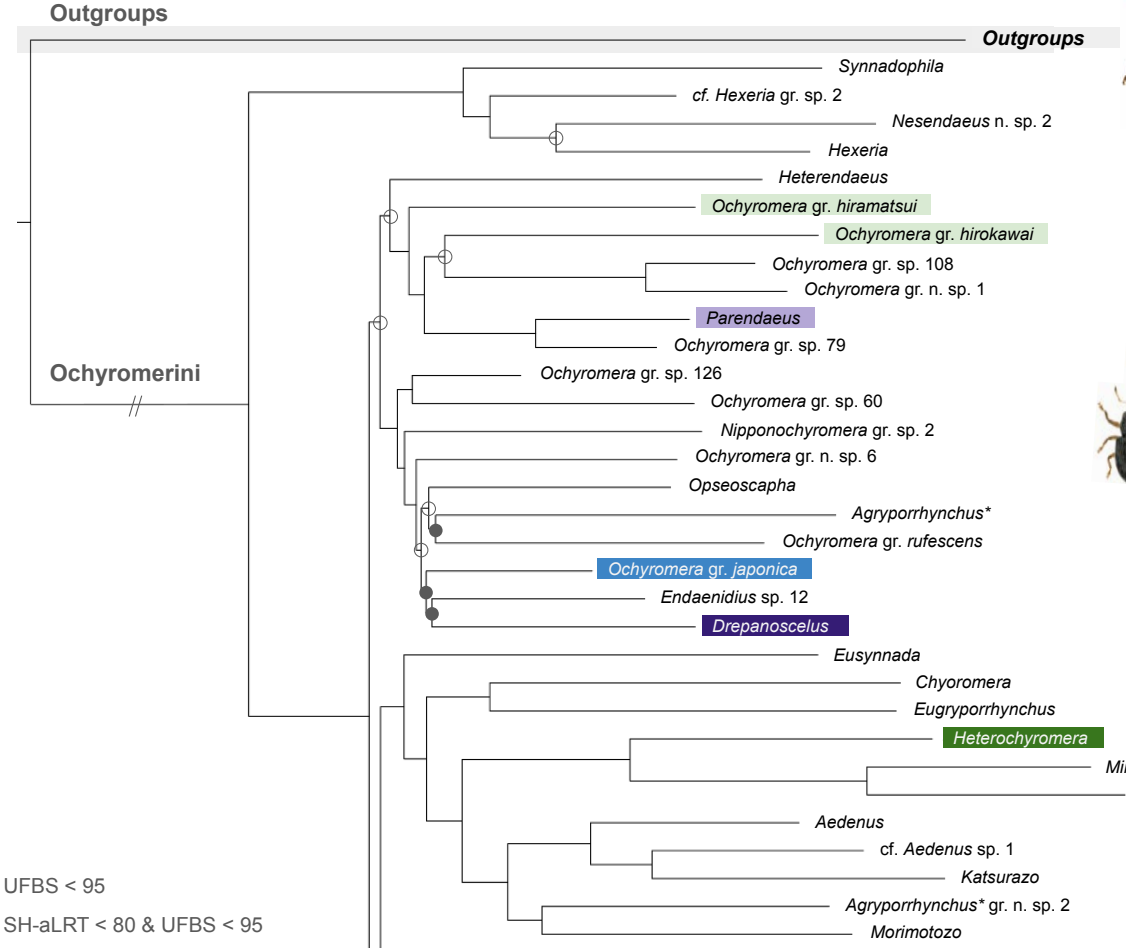
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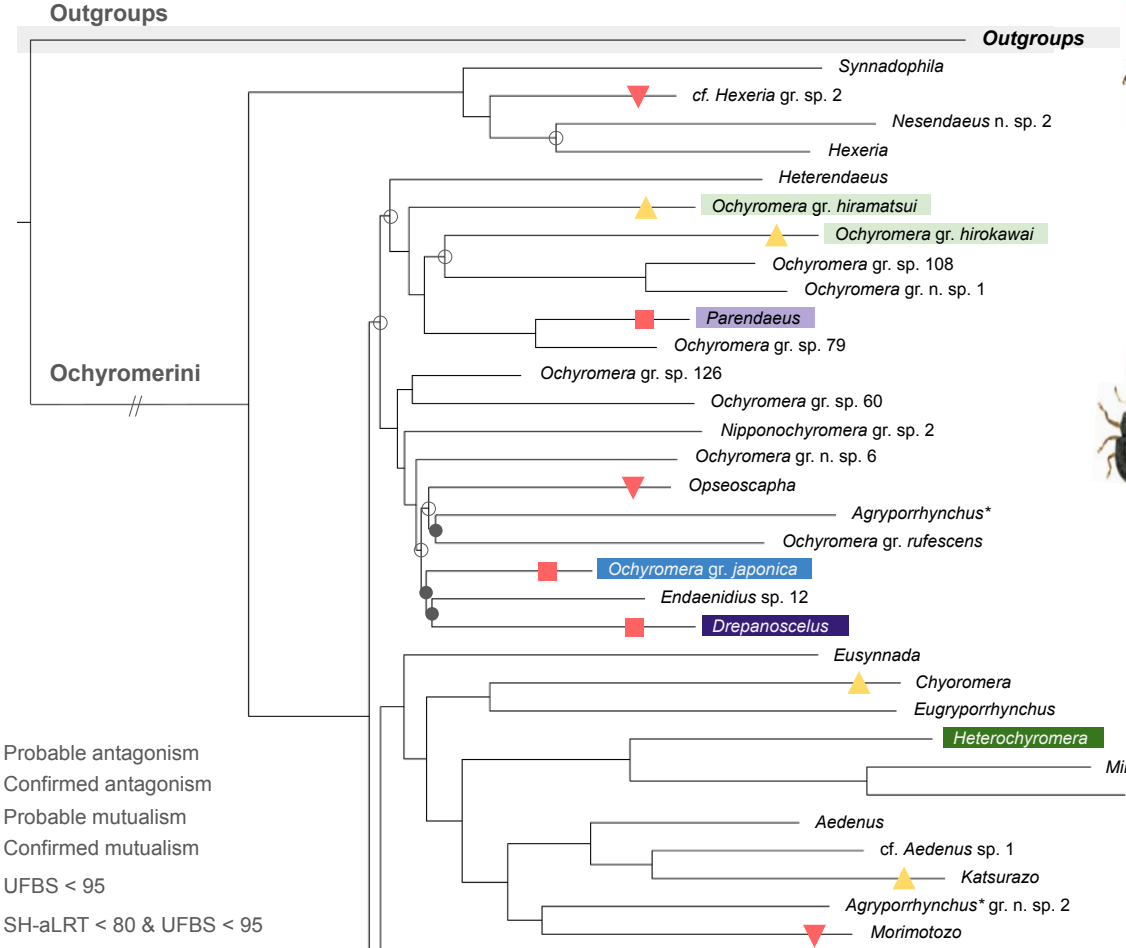
Pinaceae (Tsuga)


Podocarpaceae (Podocarpus)


Lauraceae (Litsea)


Phyllanthaceae (Glochidion)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Probable antagonism
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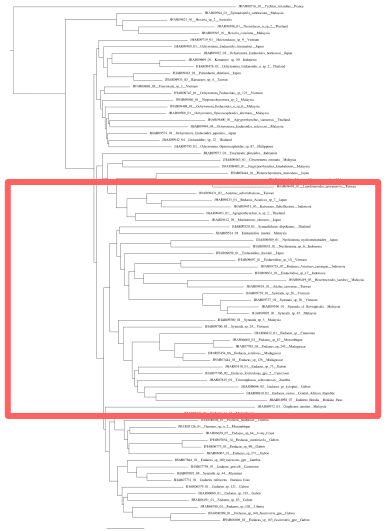

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*Synnada** gr. sp. 30
*Synnada** cf. *flavoapicalis*
*Synnada** gr. sp. 45
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Endaeus gr. sp. 124
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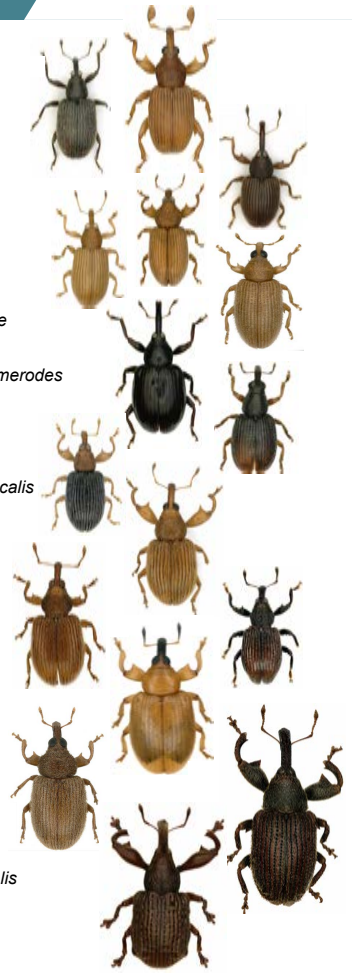
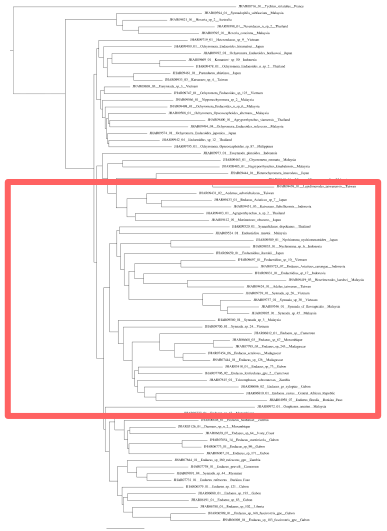
Endaeus gr. sp. 243
Endaeus gr. setulosus
Eutecheus
Endaeus gr. sp. 73
Endaeus gr. *lenticulatus*
Teinomphasus
Endaeus gr. *xylopiae*
Endaeus gr. *castus*
Endaeus gr. *floralis*
Omphasus
Endaeus gr. sp. 47
Endaeus gr. *bauhiniae*
Daeneus
Endaeus gr. sp. 64



○ UFBS < 95
● SH-aLRT < 80 & UFBS < 95



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- Confirmed antagonism
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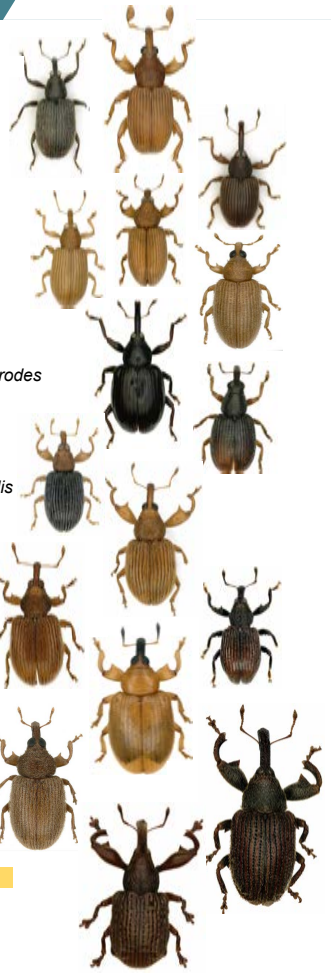

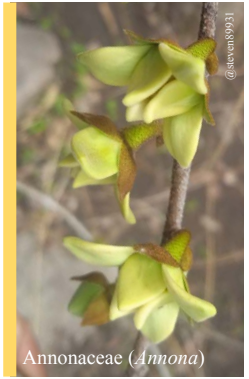

Endaeus canangae

Haran et al. 2026

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- UFBS < 95
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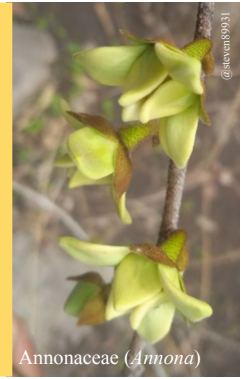
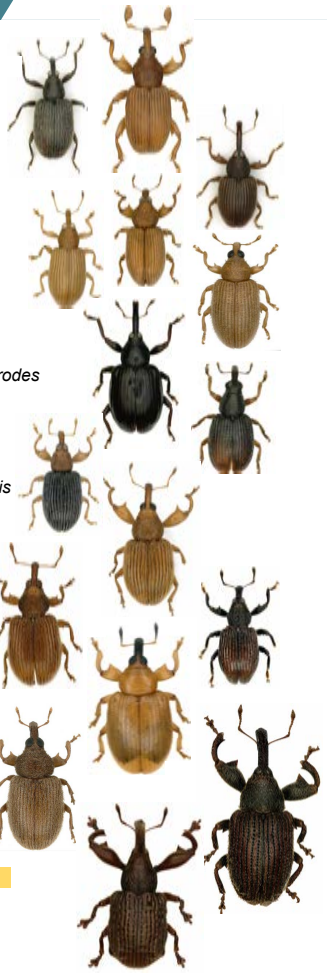


Teinomphasus

Caldara et al. 2014

cf. *Aedenus* sp. 1
Katsurazo
*Agryporrhynchus** gr. n. sp. 2
Morimotozo
Synnadichnus
Endaenidius gr. *maetoi*
*Nychiomma**
Endaenidius gr. *ikezakii*
Endaenidius sp. 10
Endaeus gr. *canangae*
Endaenidius sp. 17
Heterimerodes
Adelus
*Synnada** gr. sp. 26
*Synnada** gr. sp. 30
*Synnada** cf. *flavoapicalis*
*Synnada** gr. sp. 45
*Synnada** gr. sp. 3
*Synnada** sp. 24
Endaeus gr. sp. 124
Endaeus gr. sp. 67
Endaeus gr. sp. 243
Endaeus gr. setulosus
Eutecheus
Endaeus gr. sp. 73
Endaeus gr. *lenticulatus*
Teinomphasus
Endaeus gr. *xylopiae*
Endaeus gr. *castus*
Endaeus gr. *floralis*
Omphasus
Endaeus gr. sp. 47
Endaeus gr. *bauhiniae*
Daeneus
Endaeus gr. sp. 64



- Probable antagonism
- Confirmed antagonism
- Probable mutualism
- Confirmed mutualism
- UFBS < 95
- SH-aLRT < 80 & UFBS < 95

Nychiomma

Zhu et Kojima 2018

- Probable antagonism
- Confirmed antagonism
- Probable mutualism
- Confirmed mutualism
- UFBS < 95
- SH-aLRT < 80 & UFBS < 95

cf. *Aedenus* sp. 1
Katsurazo
*Agryporrhynchus** gr. n. sp. 2
Morimotozo
Synnadichnus
Endaenidius gr. *maetoi*
*Nychiomma**
Endaenidius gr. *ikezakii*
Endaenidius sp. 10
Endaeus gr. *canangae*
Endaenidius sp. 17
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Endaeus gr. *lenticulatus*
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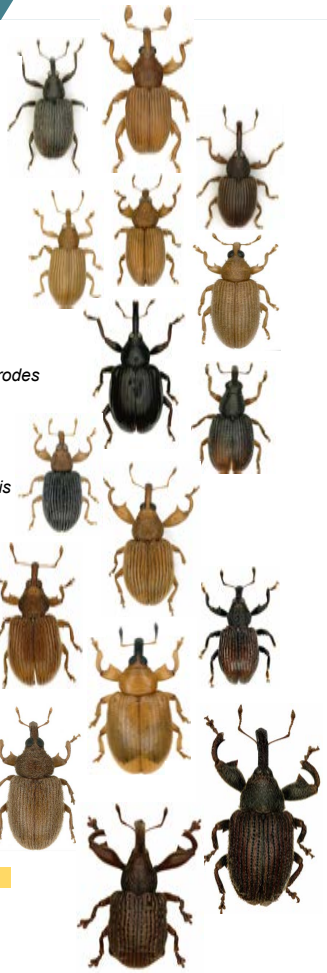
Endaeus gr. *castus*
Endaeus gr. *floralis*
Omphasus
Endaeus gr. sp. 47
Endaeus gr. *bauhiniae*
Daeneus
Endaeus gr. sp. 64



Adelus

Marshall 1926a

cf. *Aedenus* sp. 1
Katsurazo
*Agryporrhynchus** gr. n. sp. 2
Morimotozo
Synnadichnus
Endaenidius gr. *maetoi*
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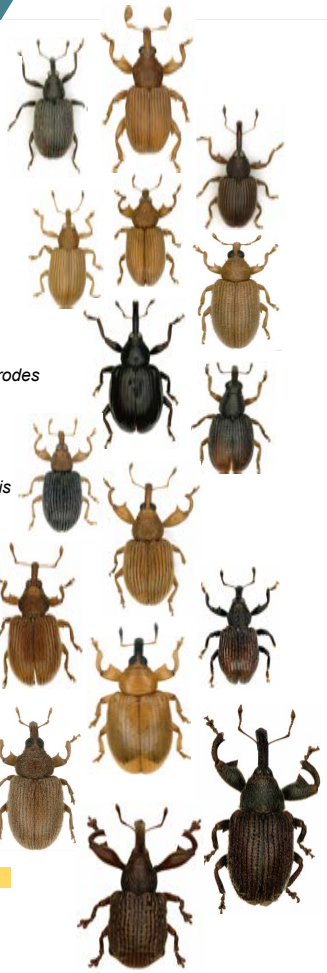
Daeneus
Endaeus gr. sp. 64



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- Confirmed antagonism
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- UFBS < 95
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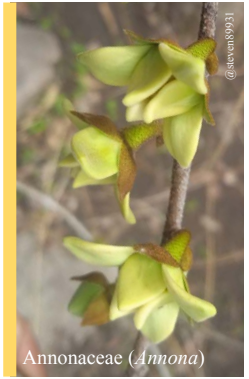
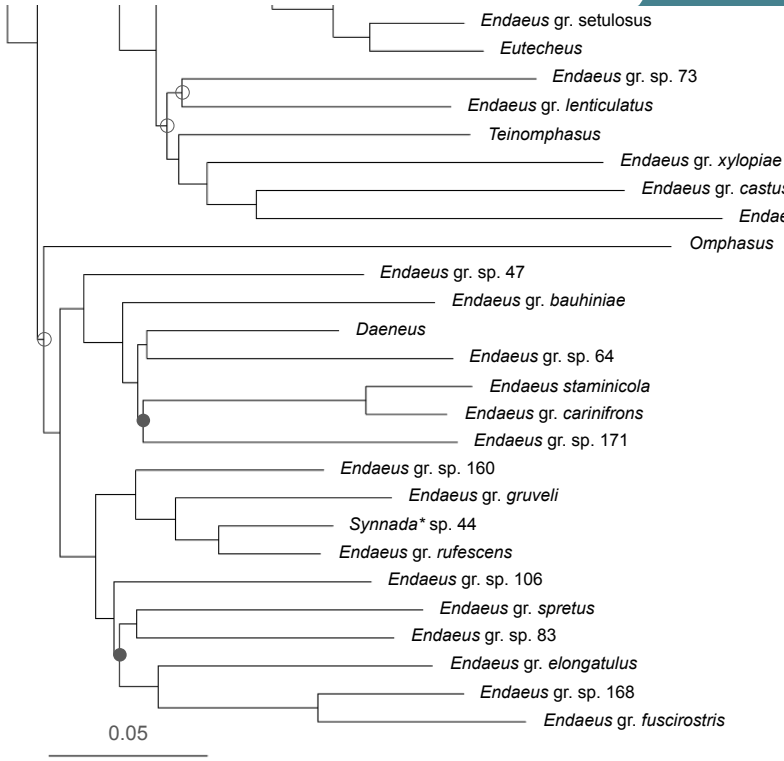
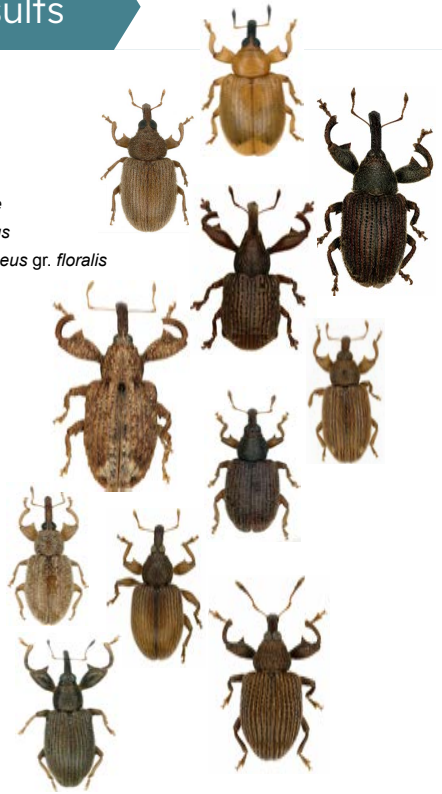
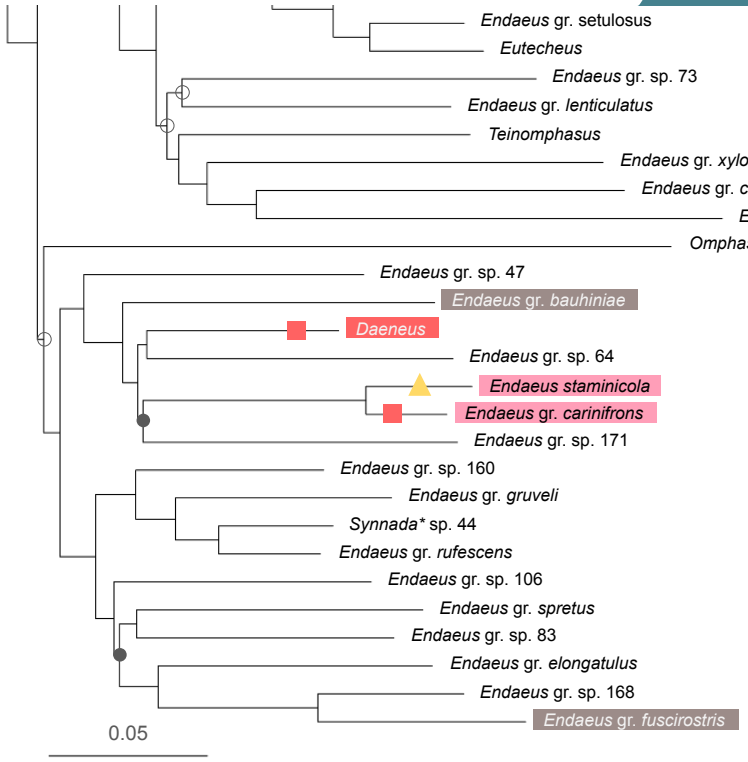


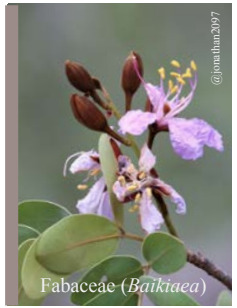




○ UFBS < 95

● SH-aLRT < 80 & UFBS < 95

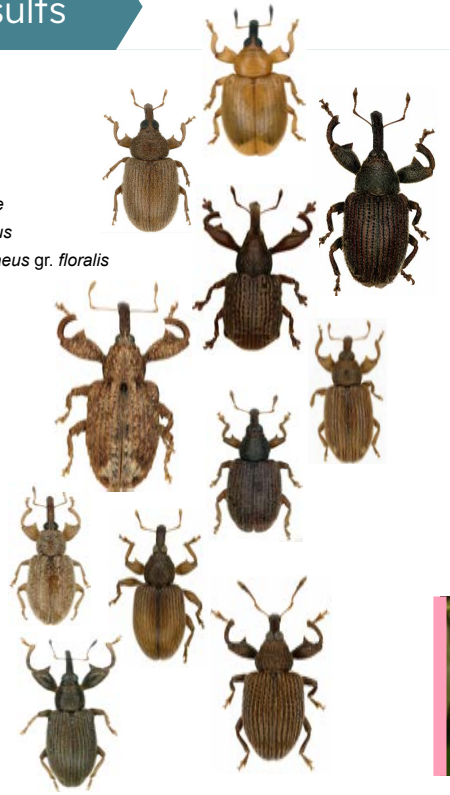


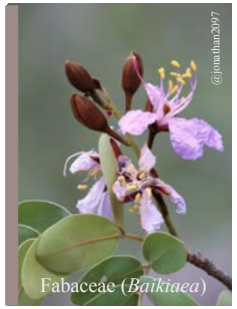


- Probable antagonism
- Confirmed antagonism
- Probable mutualism
- Confirmed mutualism
- UFBS < 95
- SH-aLRT < 80 & UFBS < 95

Endaeus staminicola

Haran et al. 2026





- Probable antagonism
- Confirmed antagonism
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- UFBS < 95
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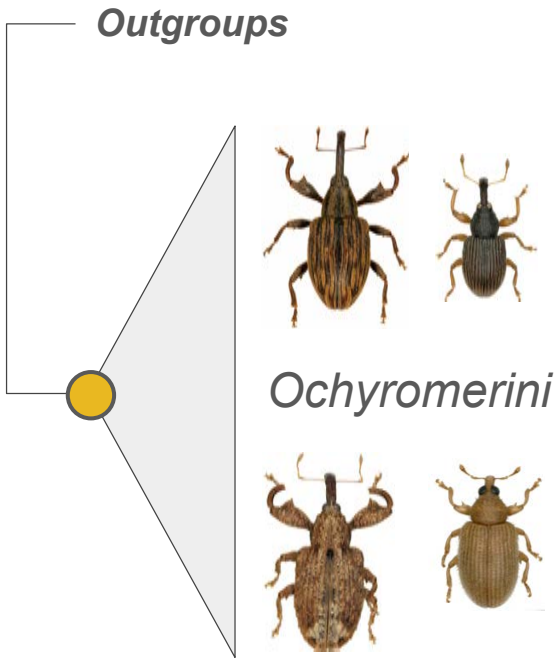
Discussion

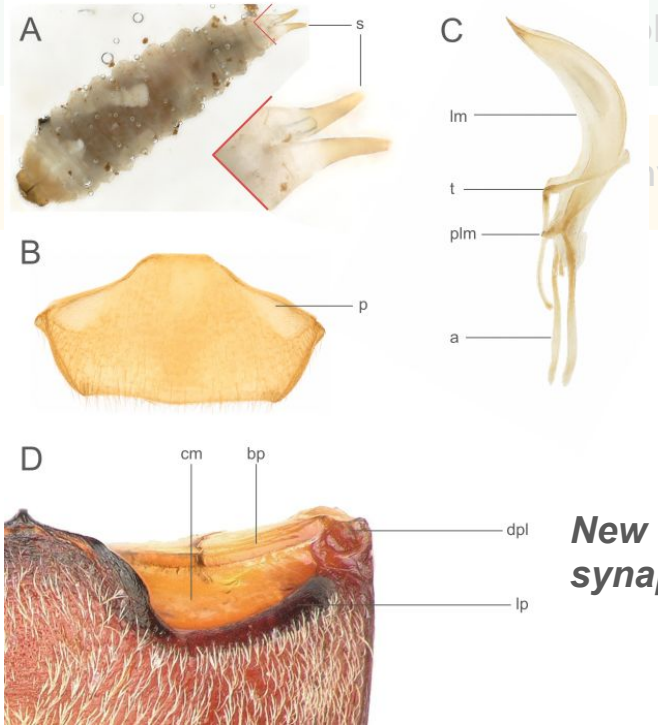
- ☐ Monophyly of Ochyromerini
- ☐ Niche conservatism of host plant families
- ☐ Monophyly of pollinating Ochyromerini

- ☐ **Monophyly of Ochyromerini**
- ☐ Niche conservatism of host plant families
- ☐ Monophyly of pollinating Ochyromerini



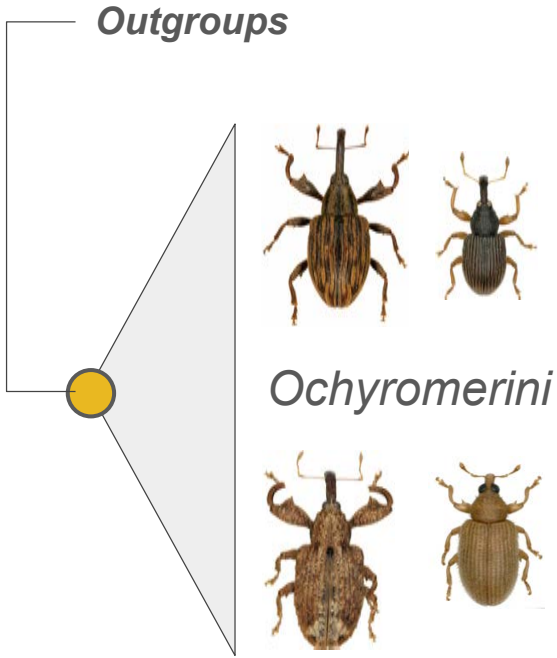
● Most recent common ancestor

☑ Monophyly of Ochyromerini



Ochyromerini synapomorphies

New synapomorphy

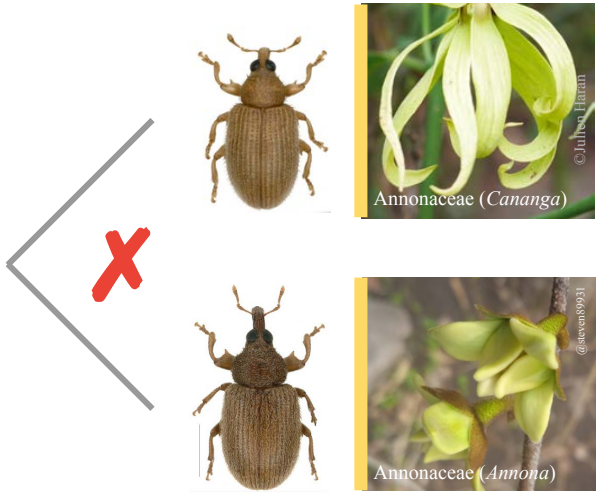


● Most recent common ancestor

- [x] Monophyly of Ochyromerini
- [ ] Niche conservatism of host plant families
- [ ] Monophyly of pollinating Ochyromerini

- ☑ Monophyly of Ochyromerini
- ? ☑ Niche conservatism of host plant families
- ☐ Monophyly of pollinating Ochyromerini

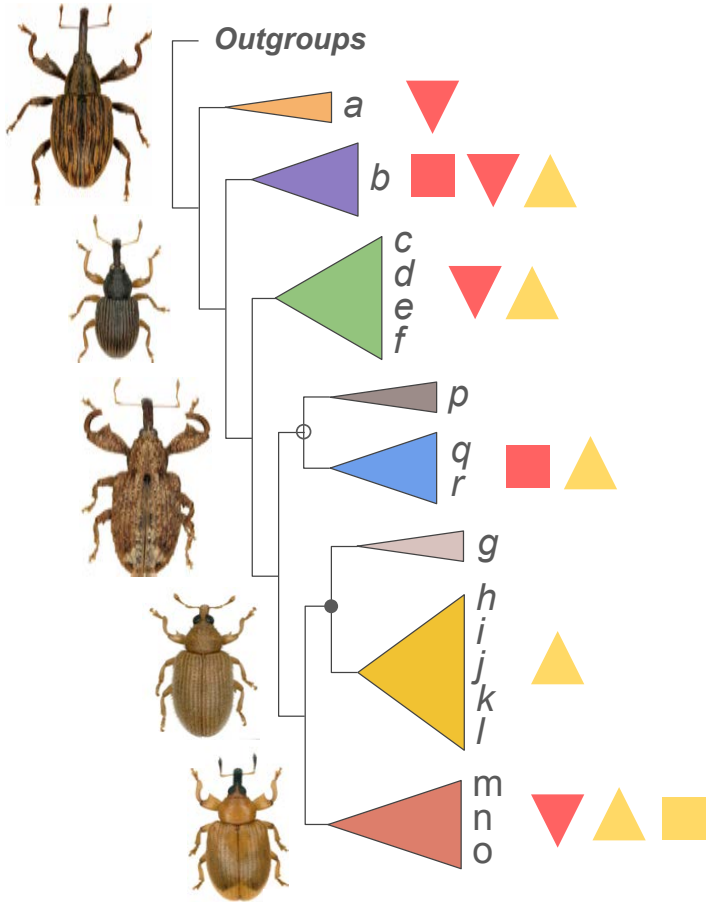
- Not enough ecological data



- **Independant** colonisation or **ancestral** association with Annonaceae?

- ☑ Monophyly of Ochyromerini
- ? ☑ Niche conservatism of host plant families
- ☐ Monophyly of pollinating Ochyromerini

- ☑ Monophyly of Ochyromerini
- ? ☑ Niche conservatism of host plant families
- ☐ Monophyly of pollinating Ochyromerini



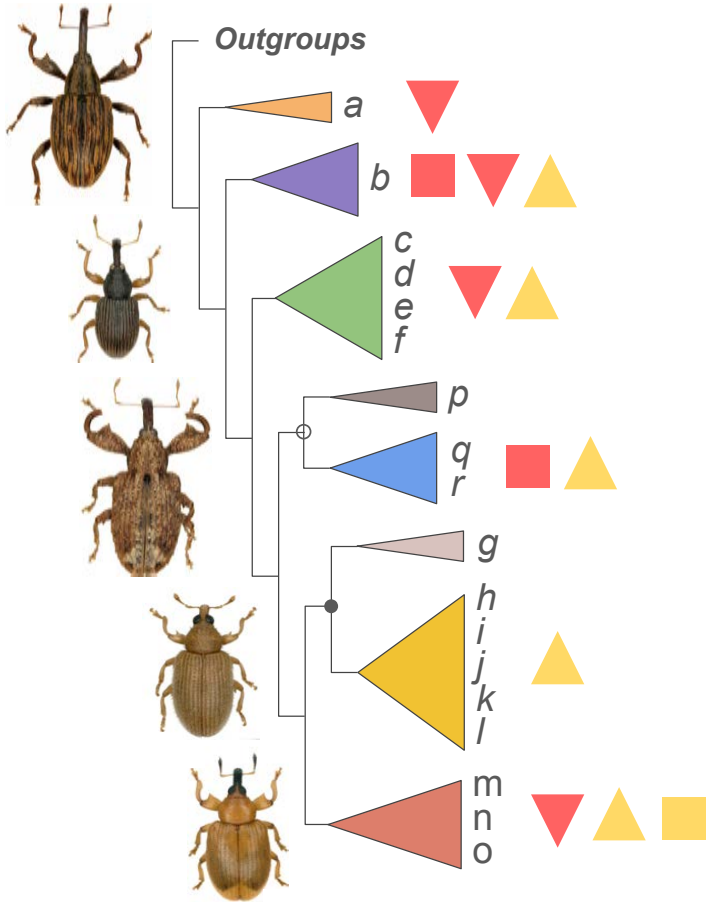
- Probable antagonism
- Confirmed antagonism
- Probable mutualism
- Confirmed mutualism

✔ Monophyly of Ochyromerini

?✔ Niche conservatism of host plant families

✗ Monophyly of pollinating Ochyromerini

- **Antagonism** and **Mutualism** much more **labile** than expected



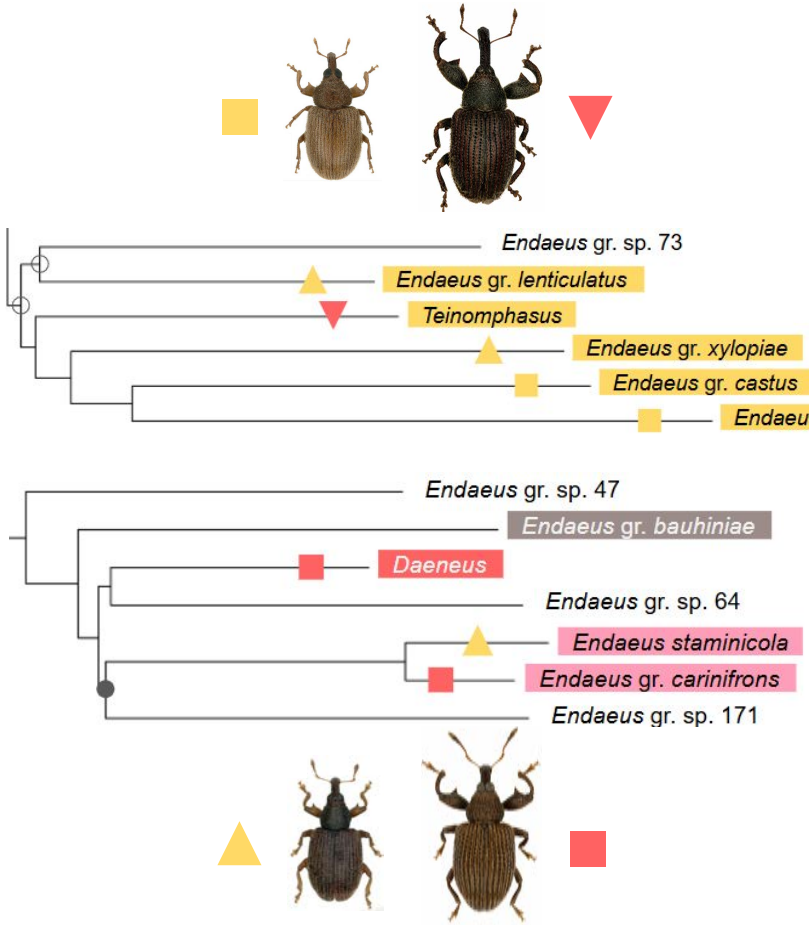
▼ Probable antagonism
■ Confirmed antagonism
▲ Probable mutualism
■ Confirmed mutualism

✔ Monophyly of Ochyromerini

?✔ Niche conservatism of host plant families

✗ Monophyly of pollinating Ochyromerini

- **Antagonism** and **Mutualism** much more **labile** than expected
- More **labile** than the **host plant conservatism**



▼ Probable antagonism

■ Confirmed antagonism

▲ Probable mutualism

■ Confirmed mutualism

✔ Monophyly of Ochyromerini

?✔ Niche conservatism of host plant families

✘ Monophyly of pollinating Ochyromerini

- **Lability** of the **antagonism** - **mutualism** spectrum
- Morphological **convergence** between pollinated plants
- High number of **plant families** involved

☑ Monophyly of Ochyromerini

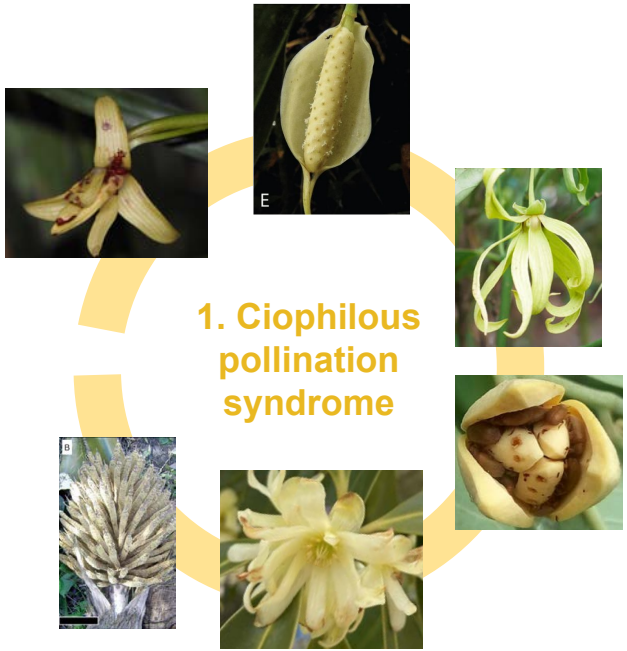
☑ Niche conservatism of host plant families

☒ Monophyly of pollinating Ochyromerini

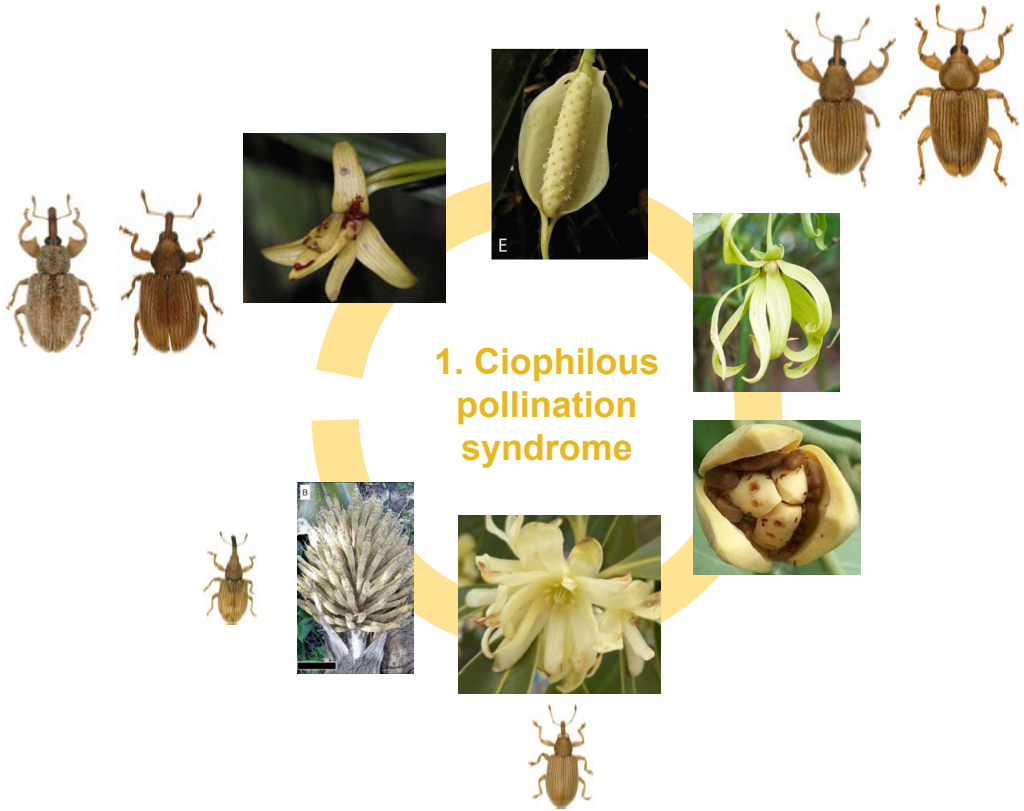
☐ Evolution through **ecological opportunities** driven by **pollination syndromes**

- **Lability** of the **antagonism** - **mutualism** spectrum
- Morphological **convergence** between pollinated plants
- High number of **plant families** involved

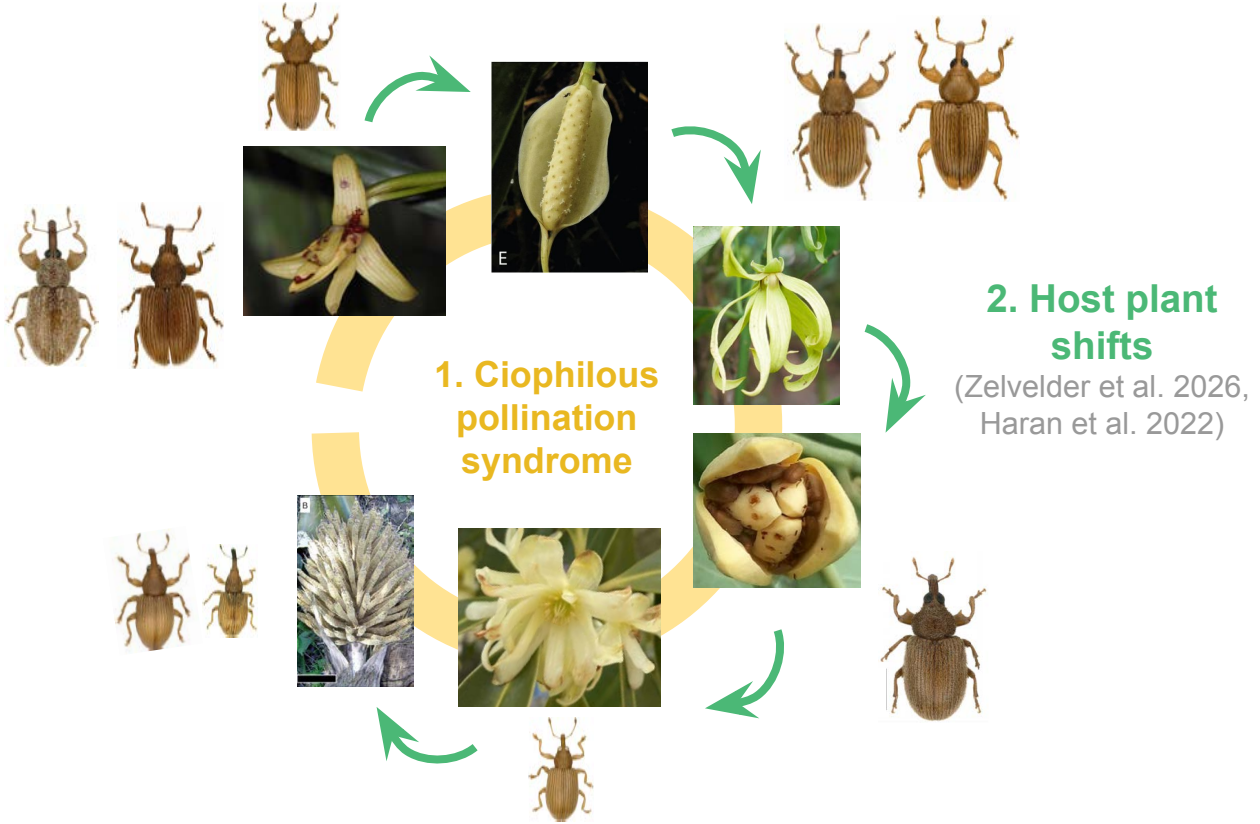
- Evolution through **ecological opportunities** driven by **pollination syndromes**



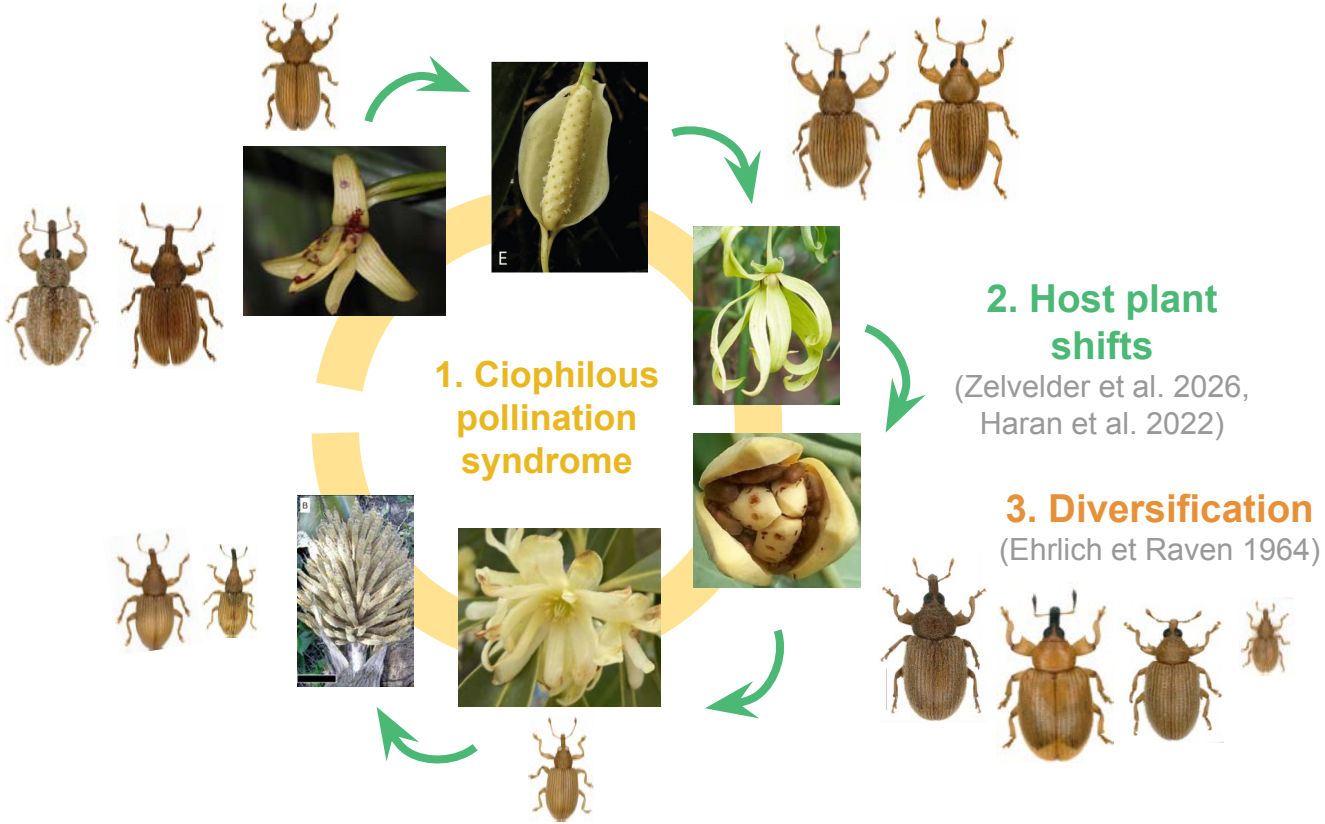
Evolution through **ecological opportunities** driven by **pollination syndromes**



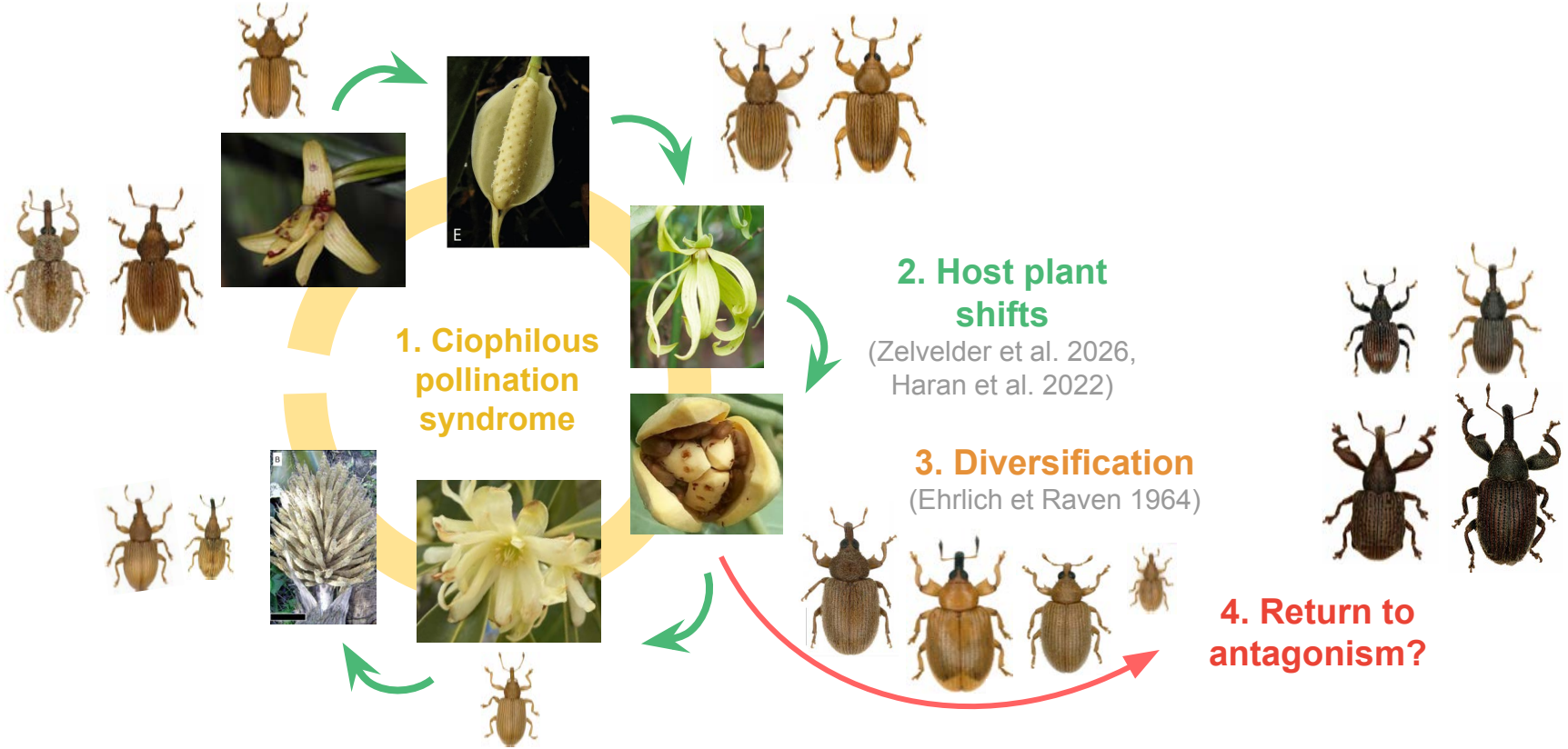
Evolution through **ecological opportunities** driven by **pollination syndromes**



Evolution through **ecological opportunities** driven by **pollination syndromes**



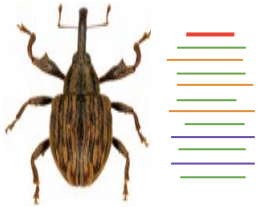
Evolution through **ecological opportunities** driven by **pollination syndromes**



Conclusion

A new method and set of markers

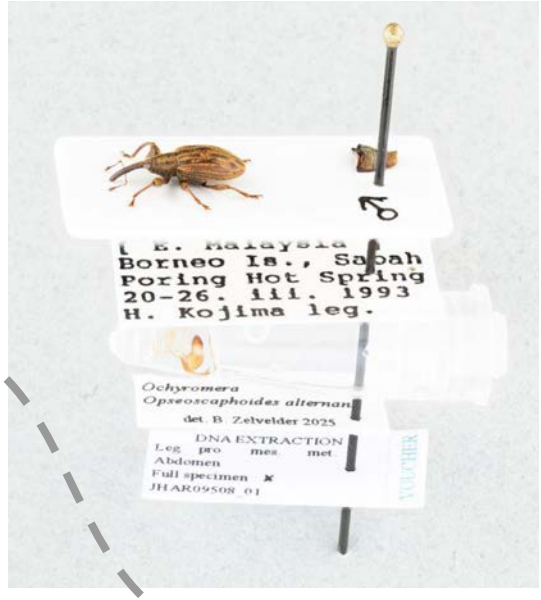
GENOME ALIGNMENT-
GABBI
-BASED BAIT INFERENCE



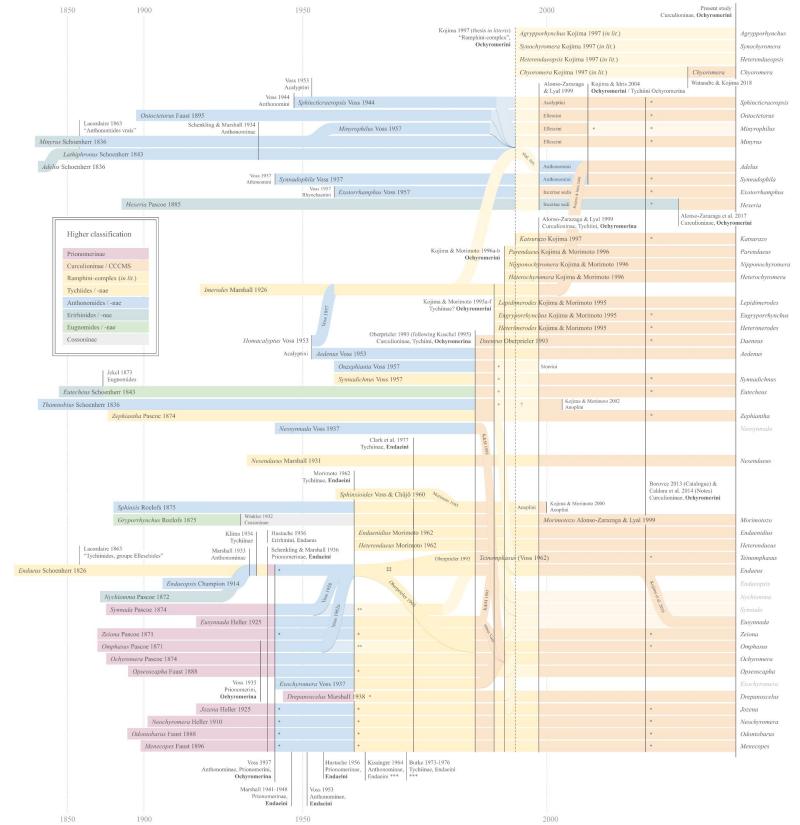
New set of **shared homologous regions (SHR)** for target enrichment of **weevils** (Coleoptera, Curculionoidea)

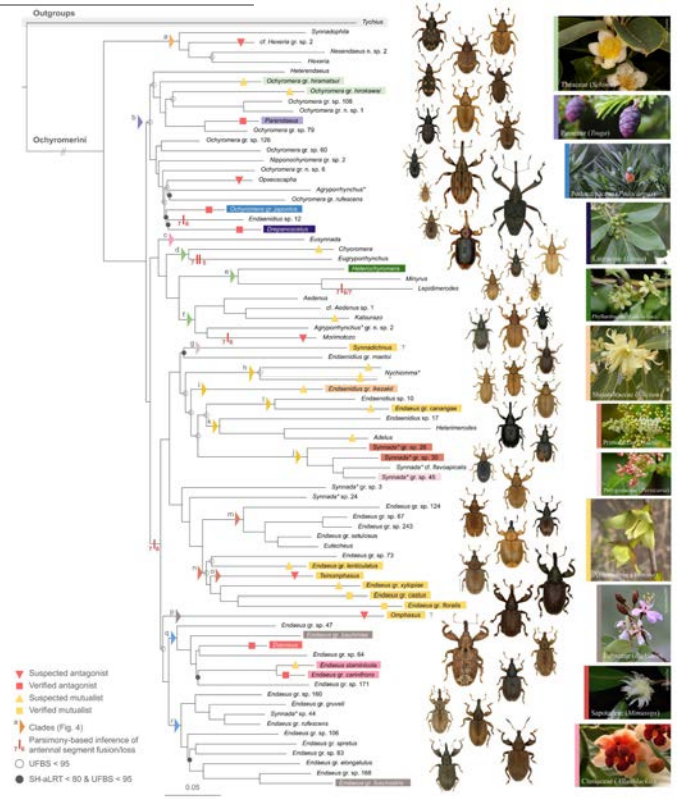
Fully **automated** and **open-source** pipeline available on Github

The importance of entomological collections



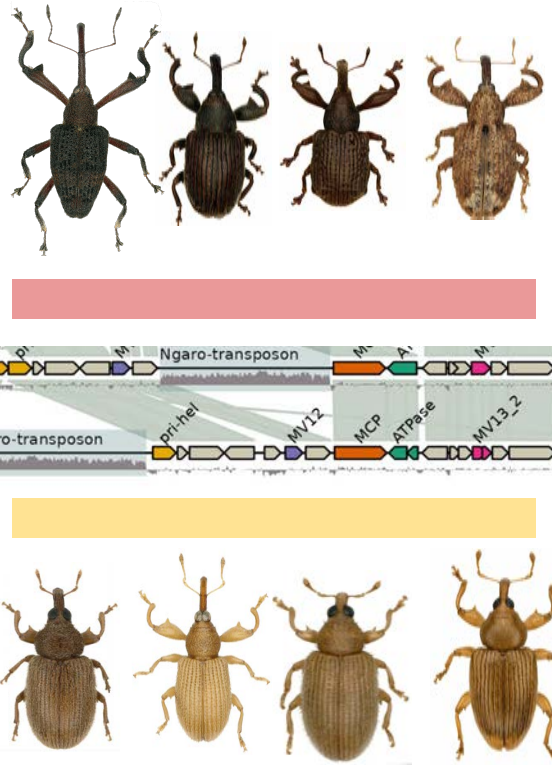
A leap in our knowledge of Ochyromerini





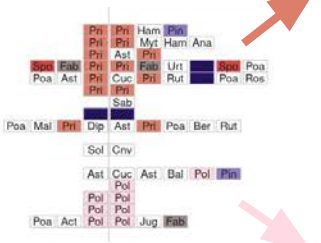
Perspectives

- **Genomic** signature of morphological convergence and mutualist lifestyle



Perspectives

- **Genomic** signature of morphological convergence and mutualist lifestyle
- Many **ecological** interactions to discover

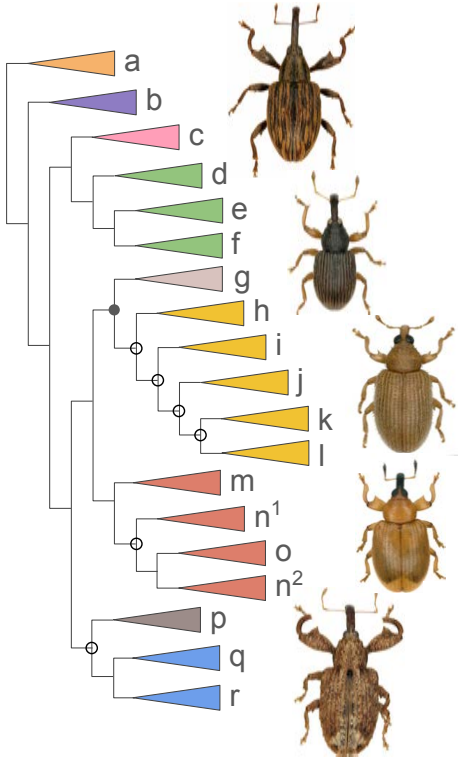



Primulaceae (*Maesa*)


Polygonaceae (*Persicaria*)

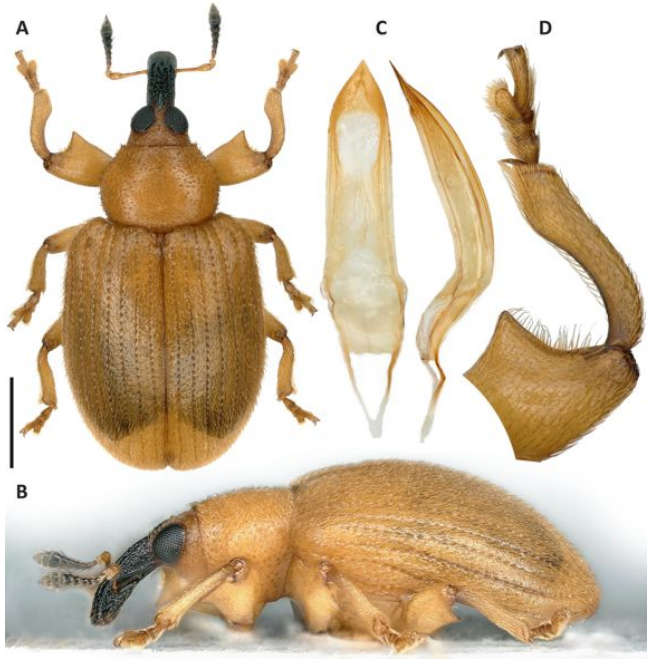
Perspectives

- **Genomic** signature of morphological convergence and mutualist lifestyle
- Many **ecological** interactions to discover
- Improving **phylogenomic** inferences



Perspectives

- **Genomic** signature of morphological convergence and mutualist lifestyle
- Many **ecological** interactions to discover
- Improving **phylogenomic** inferences
- **Taxonomic** and **systematic** revision of Ochyromerini



Haran et al. 2026

Acknowledgments








Kéo Gengembre

CBGP Centre de Biologie pour la Gestion des Populations











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isem
Institut des Sciences de l'Evolution-Montpellier

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INRAE

anr

UNIVERSITÉ MONTPELLIER

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anr
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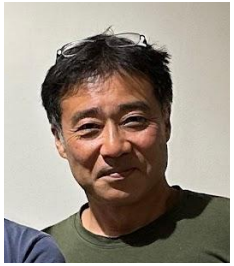
CBGP Centre de Biologie pour la Gestion des Populations
FOUNDED IN 1891
TOKYO UNIVERSITY OF AGRICULTURE











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anr
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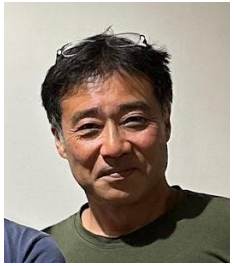
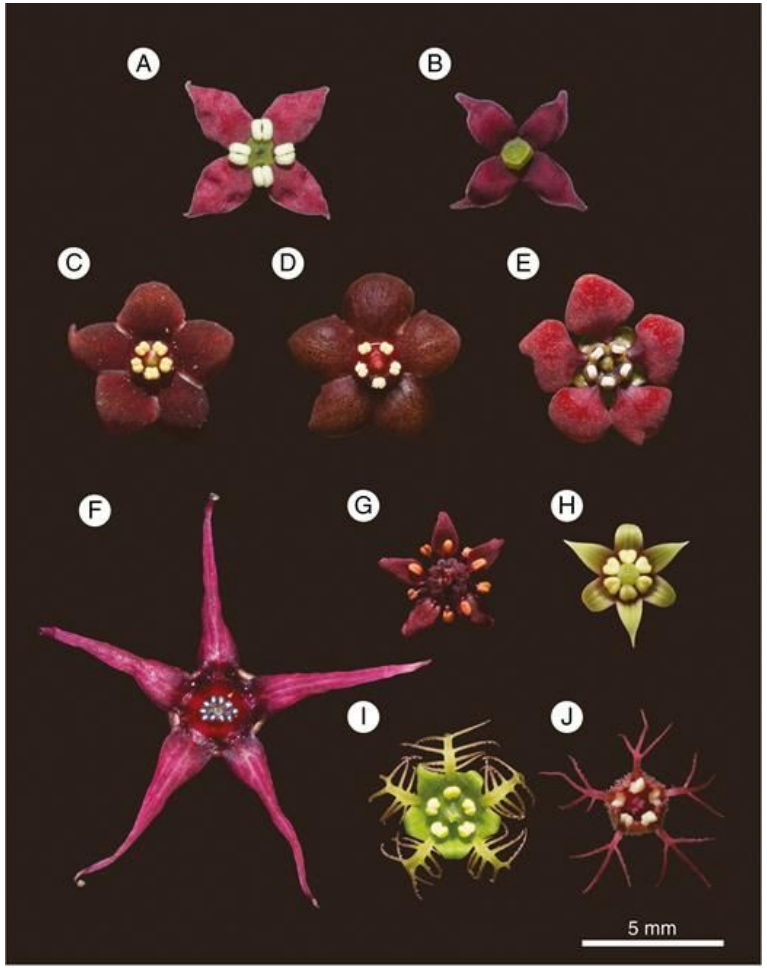
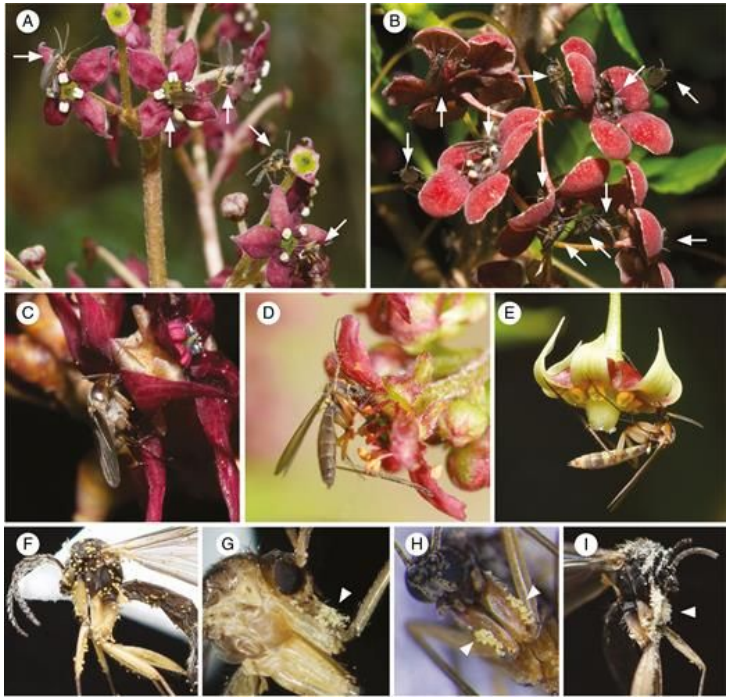

CBGP Centre de Biologie pour la Gestion des Populations
cirad
Natural History Museum
CSIRO
canadian museum of nature
nature
musée canadien de la nature
SWEDISH MUSEUM OF NATURAL HISTORY
MUSÉUM NAL HIST NATURELLE
FOUNDED IN 1891
TOKYO UNIVERSITY OF AGRICULTURE

Thank you for your attention!

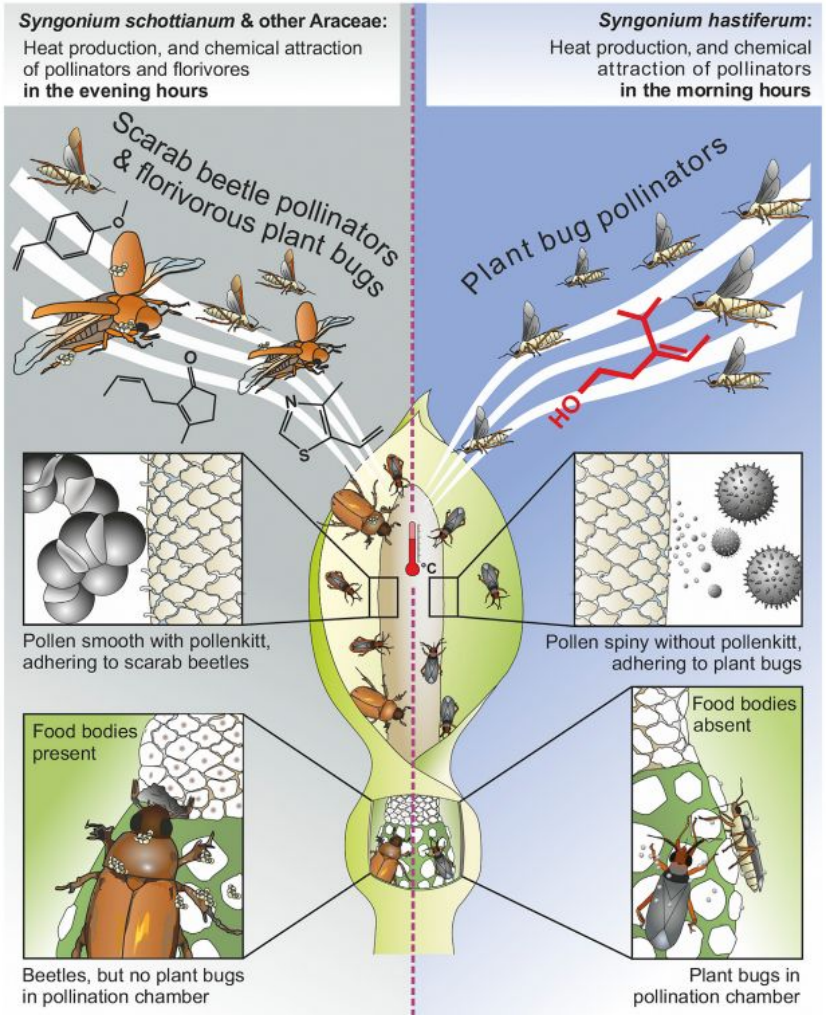
ANNEXES



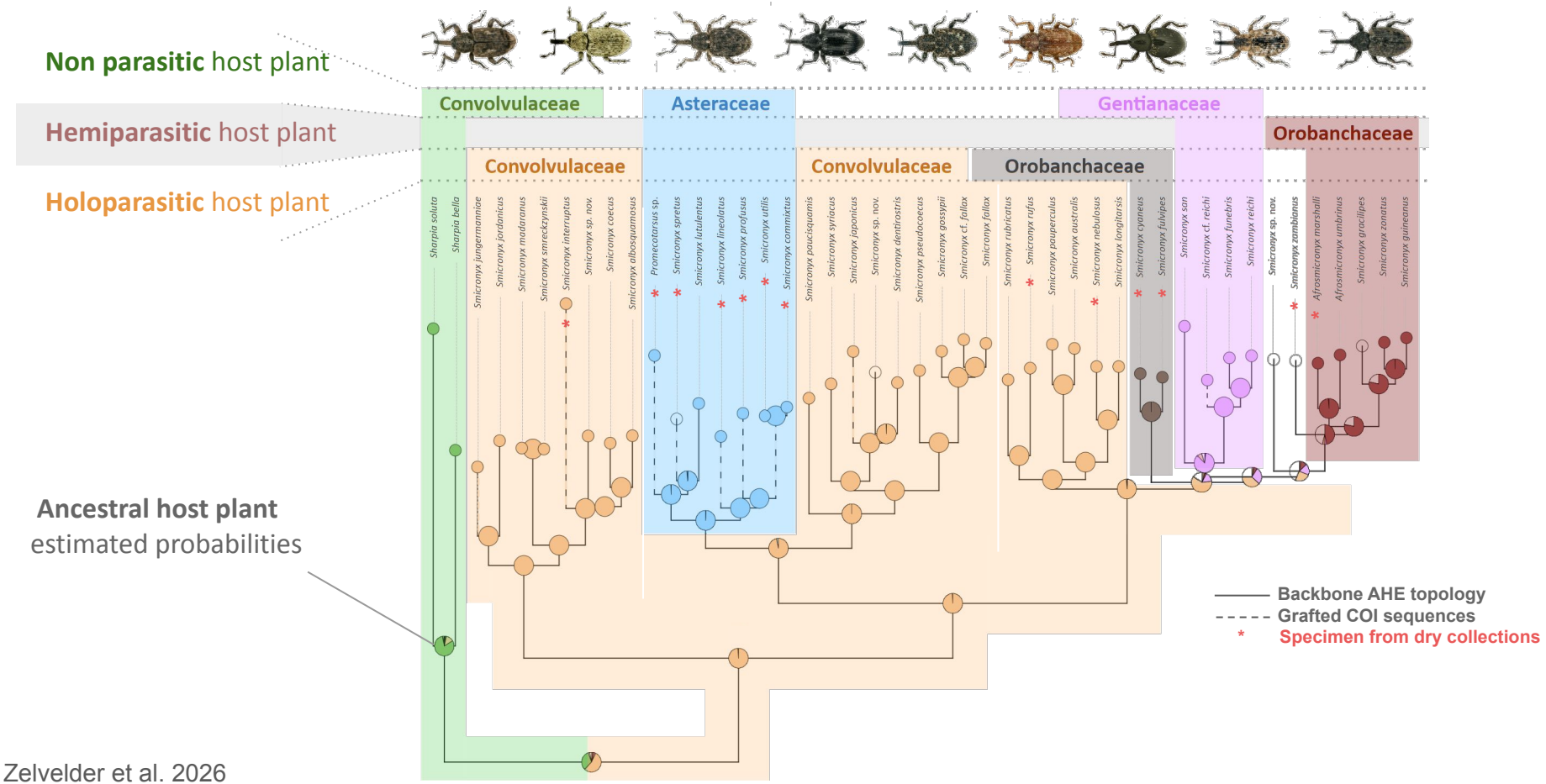


Aucuba japonica (Garryaceae),
Euonymus spp. (Celastraceae),
Disanthus cercidifolius (Hamamelidaceae),
Micranthes fusca (Saxifragaceae),
Streptopus streptopoides (Liliaceae)

Mochizuki et Kawakita 2018

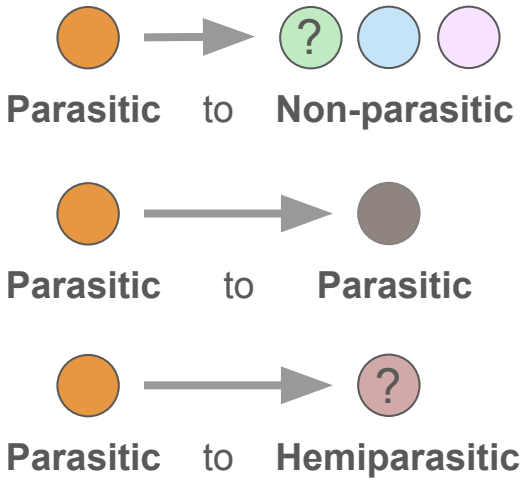


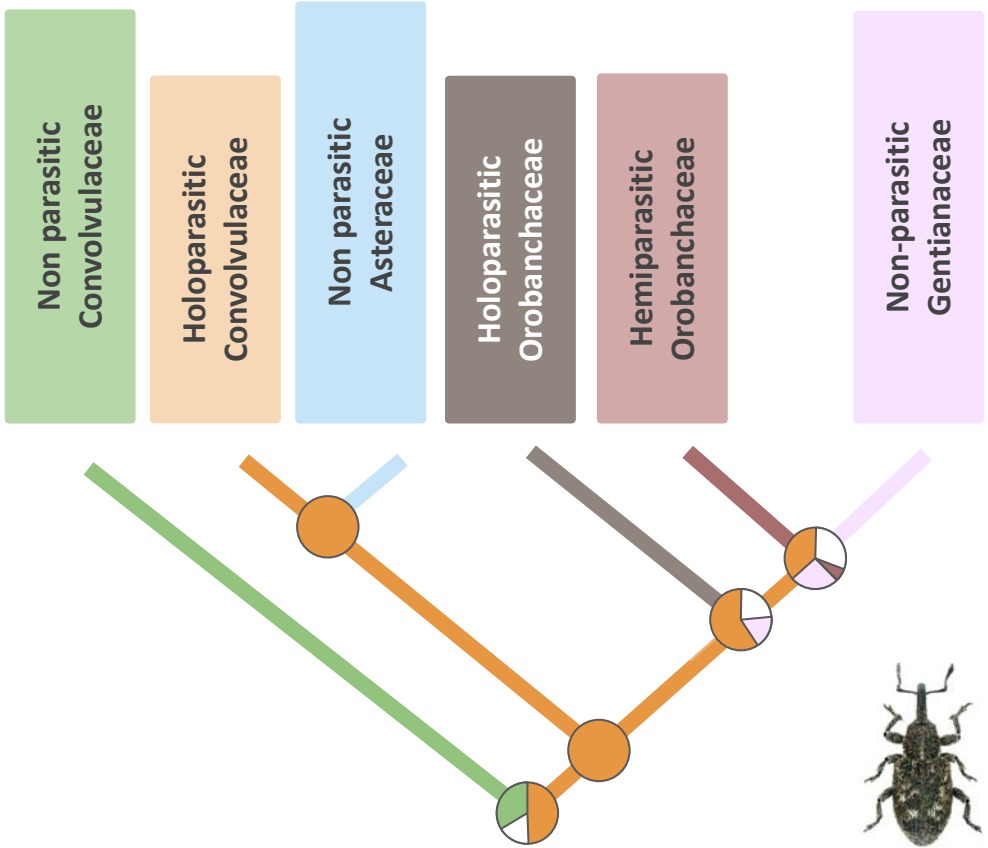
Etl et al. 2022



Zelvelder et al. 2026

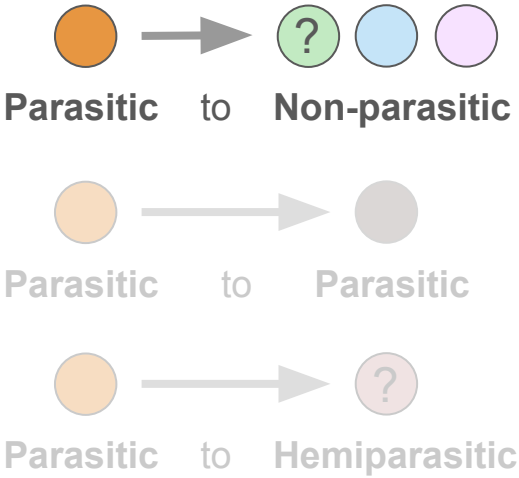
Host plant shifts inferred:

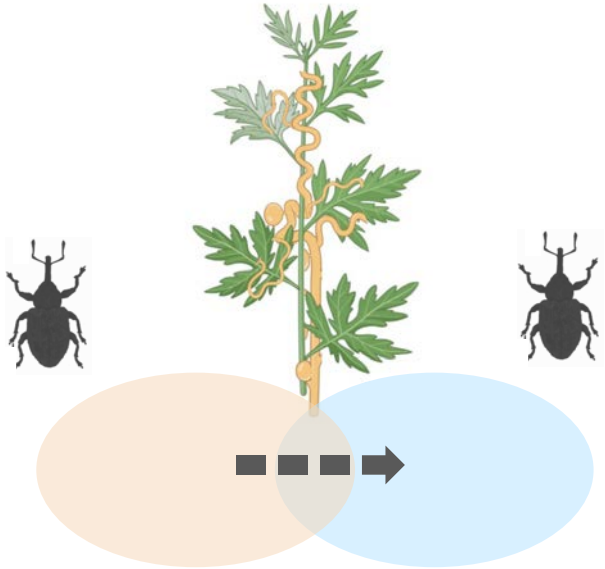




Zelvelder et al. 2026

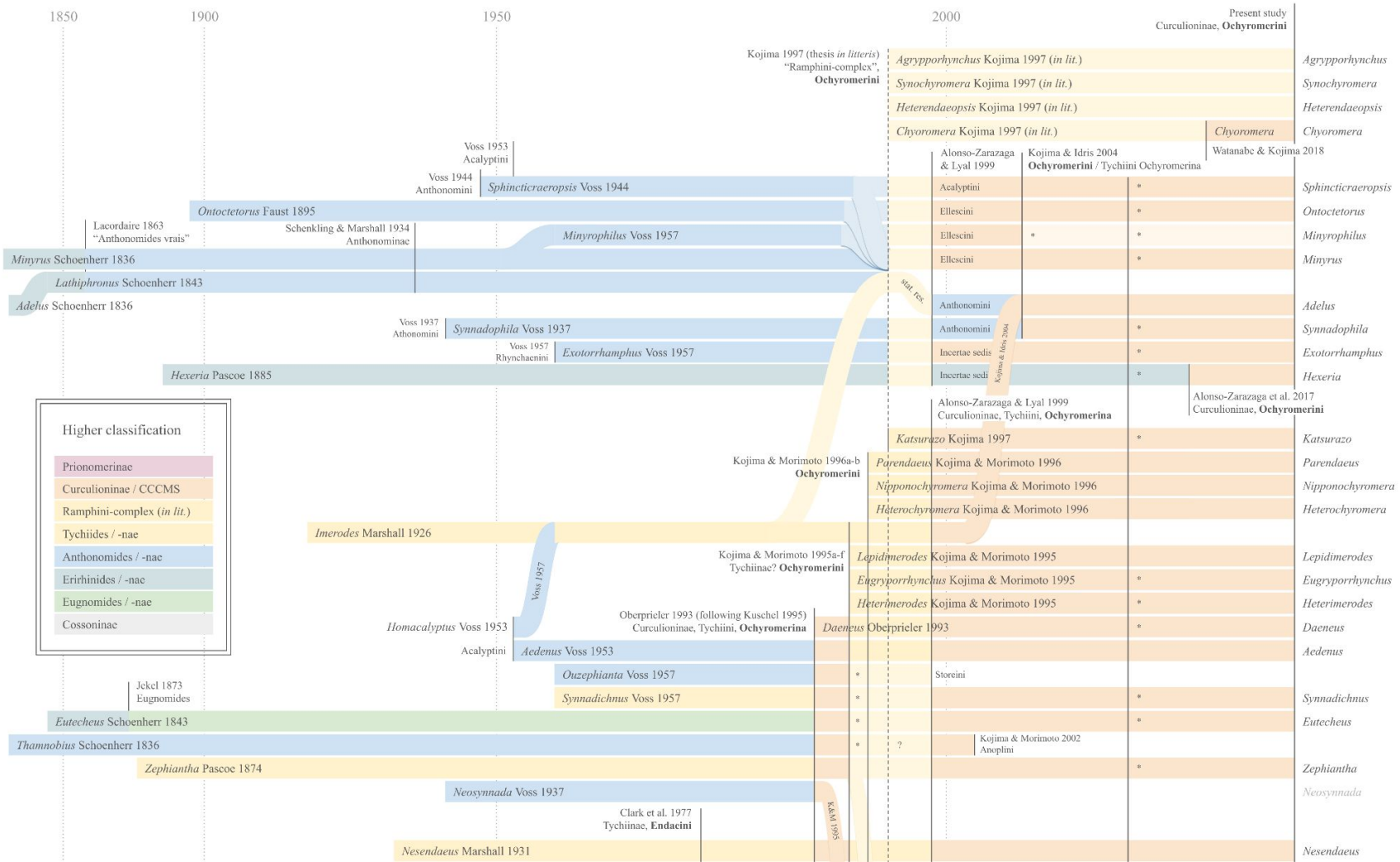
Host plant shifts inferred:

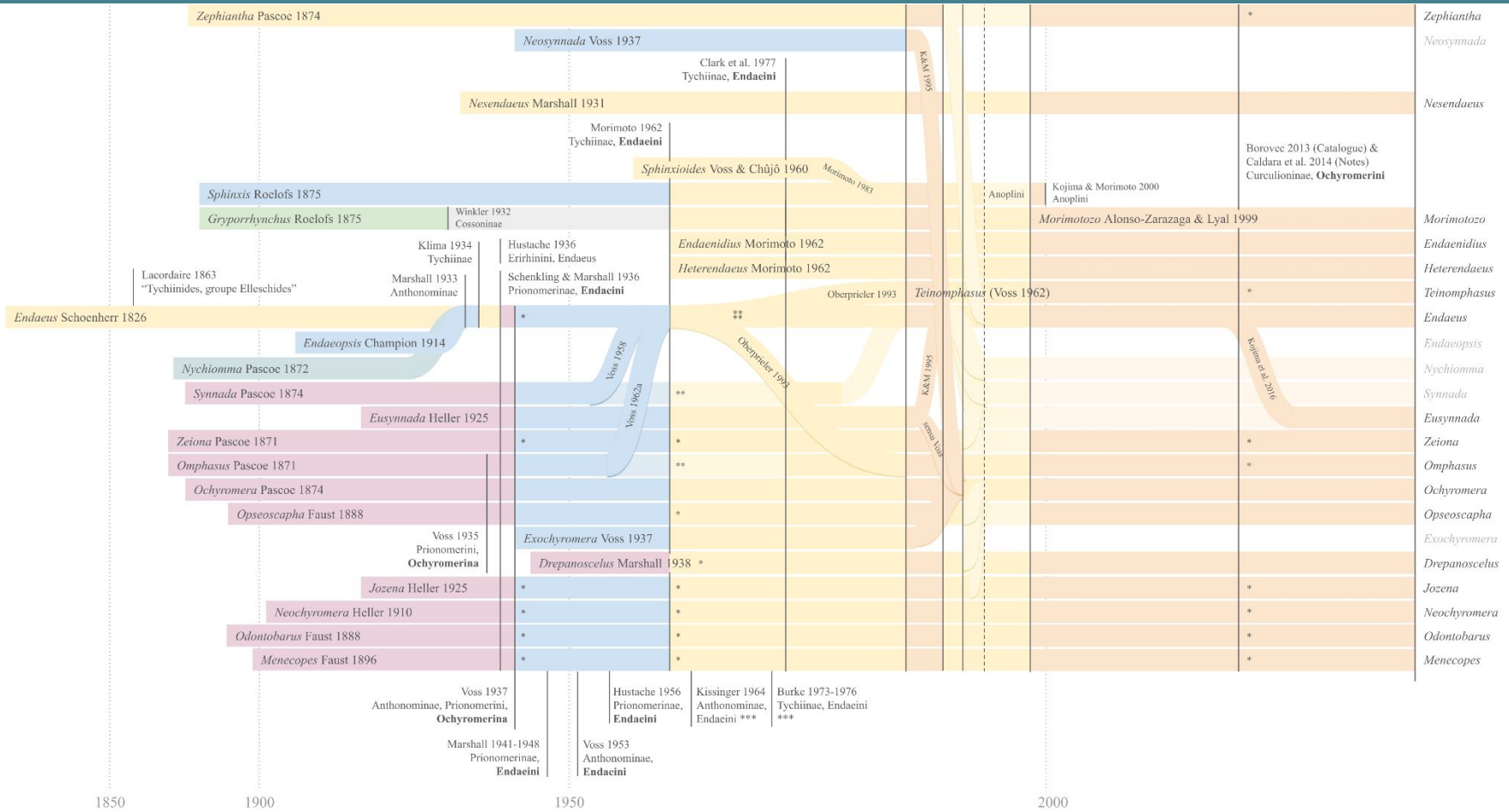




- Spatial ✅
- Temporal ✅
- Detection ✅
- Structural ✅
- Chemical ✅

= ecological opportunity that can lead to **host plant shifts**


1850
1900
1950
2000
Present study
Curculioninae, Ochyromerini
Kojima 1997 (thesis in litteris)
"Ramphini-complex",
Ochyromerini
Agrypporhynchus Kojima 1997 (in lit.)
Synochyromera Kojima 1997 (in lit.)
Heterendaeopsis Kojima 1997 (in lit.)
Chyoromera Kojima 1997 (in lit.)
Chyoromera
Watanabe & Kojima 2018
Agrypporhynchus
Synochyromera
Heterendaeopsis
Chyoromera
Voss 1953
Acalyptini
Voss 1944
Anthonomini
Sphincticraeopsis Voss 1944
Alonso-Zarazaga
& Lyal 1999
Kojima & Idris 2004
Ochyromerini / Tychiini Ochyromerina
Acalyptini
Sphincticraeopsis
Ontoctetorus Faust 1895
Ellescini
Ontoctetorus
Lacordaire 1863
"Anthonomides vrais"
Schenkling & Marshall 1934
Anthonominae
Minyrophilus Voss 1957
Ellescini
Minyrophilus
Minyrus Schoenherr 1836
Ellescini
Minyrus
Lathiphronus Schoenherr 1843
stat. res.
Adelus Schoenherr 1836
Anthonomini
Adelus
Voss 1937
Athonomini
Synnadophila Voss 1937
Anthonomini
Synnadophila
Voss 1957
Rhynchaenini
Exotorrhamphus Voss 1957
Incertae sedis
Exotorrhamphus
Hexeria Pascoe 1885
Incertae sedi
Kojima & Idris 2004
Hexeria
Alonso-Zarazaga et al. 2017
Curculioninae, Ochyromerini
Alonso-Zarazaga & Lyal 1999
Curculioninae, Tychiini, Ochyromerina
Katsurazo Kojima 1997
Katsurazo
Kojima & Morimoto 1996a-b
Ochyromerini
Parendaeus Kojima & Morimoto 1996
Nipponochyromera Kojima & Morimoto 1996
Heterochyromera Kojima & Morimoto 1996
Parendaeus
Nipponochyromera
Heterochyromera
Imerodes Marshall 1926
Kojima & Morimoto 1995a-f
Tychiinae? Ochyromerini
Lepidimerodes Kojima & Morimoto 1995
Eugryporrhynchus Kojima & Morimoto 1995
Heterimerodes Kojima & Morimoto 1995
Lepidimerodes
Eugryporrhynchus
Heterimerodes
Voss 1957
Oberprieler 1993 (following Kuschel 1995)
Curculioninae, Tychiini, Ochyromerina
Homacalyptus Voss 1953
Daeneus Oberprieler 1993
Daeneus
Acalyptini
Aedenus Voss 1953
Aedenus
Ouzephianta Voss 1957
Storeini
Synnadichnus Voss 1957
Synnadichnus
Jekel 1873
Eugnomides
Eutecheus Schoenherr 1843
Eutecheus
Thamnobius Schoenherr 1836
Kojima & Morimoto 2002
Anoplini
Zephiantha Pascoe 1874
Zephiantha
Neosynnada Voss 1937
Neosynnada
K&M 1995
Clark et al. 1977
Tychiinae, Endacini
Nesendaeus Marshall 1931
Nesendaeus
Higher classification
Prionomerinae
Curculioninae / CCCMS
Ramphini-complex (in lit.)
Tychiides / -nae
Anthonomides / -nae
Erirhinides / -nae
Eugnomides / -nae
Cossoninae

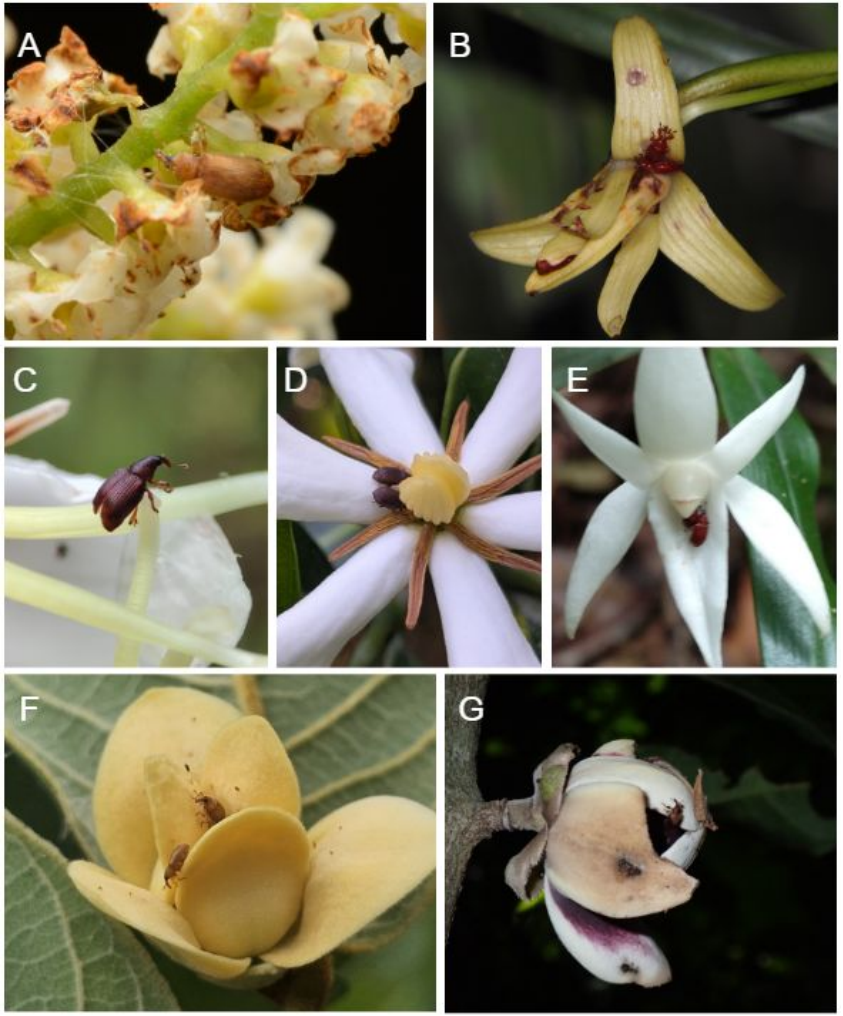


* Those genera were omitted by the author (*i.e.* due to a geographic restriction of the publication) but should follow the taxonomic reassignation of the tribe.

** It is unclear why these genera were not treated by K. Morimoto. He might have omitted them because they have been already synonymised to *Endaeus* by Voss or because they do not occur in Japan. Similarly, Clark *et al.* 1977 consider these genera to be valid regardless of the synonymy formulated by Voss, which makes *Synnada* appear as a synonym of *Endaeus* in Oberprieler 1993 but not in Clark *et al.* 1977.

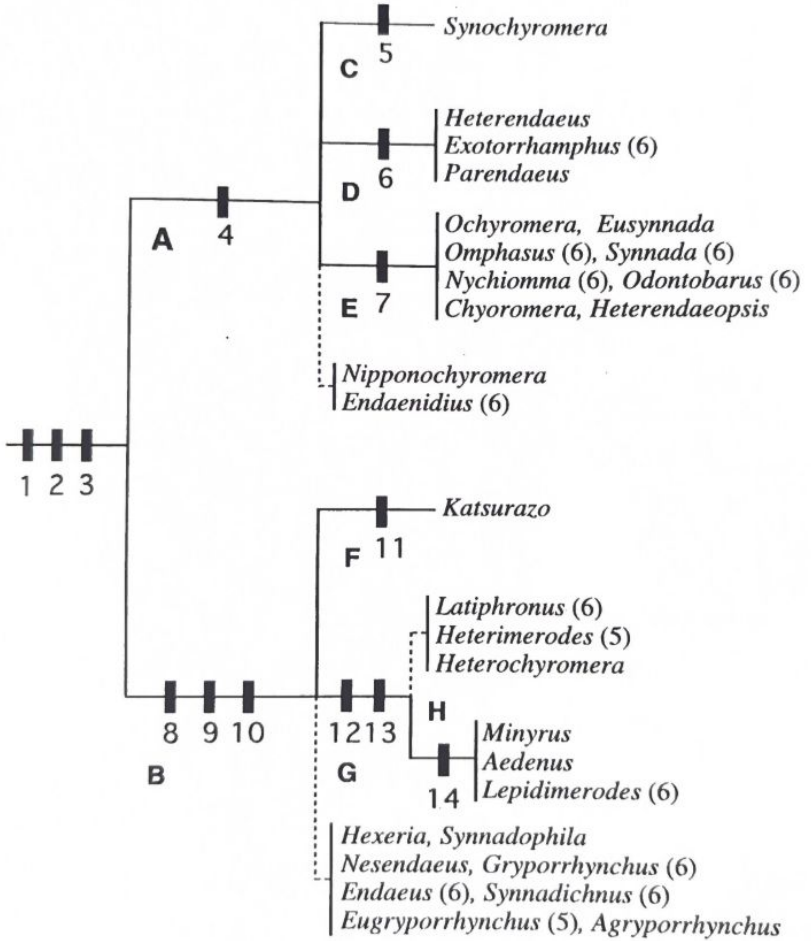
*** Kissinger transferred many genera from Tychiini to Endaeini (Anthonominae) in a broad sense, including Lignyodini and Ellescini. For its complexity and brevity, this event is not represented on this timeline.

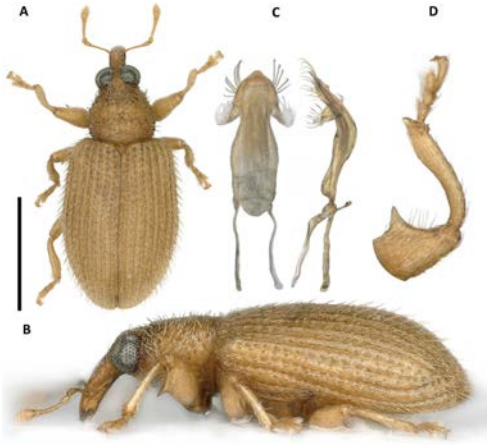
⁂ Hoffmann (1968) suggested that the genus *Endaeus* was better placed within the Anthonomini rather than the Tychiini, without further consideration



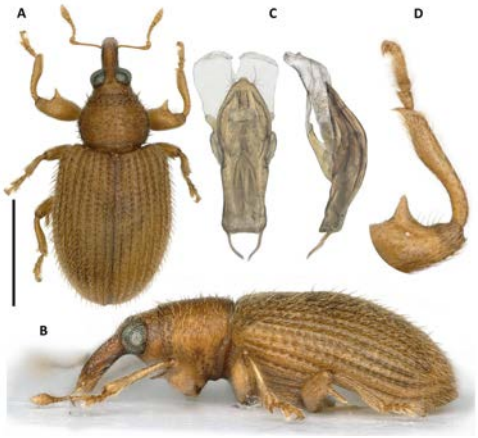
iNaturalist


A
B
V1
V2
V3
V4
V5

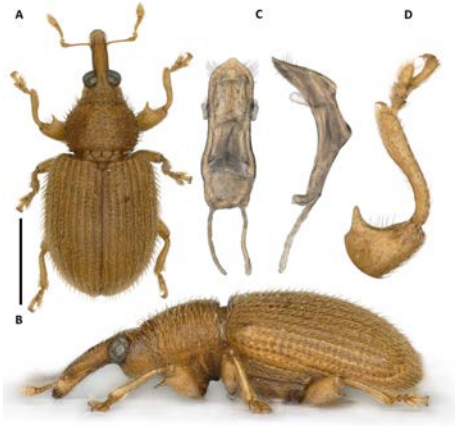

Synochyromera
5
C
Heterendaeus
Exotorrhamphus (6)
Parendaeus
6
D
A
4
Ochyromera, Eusynnada
Omphasus (6), Synnada (6)
Nychiomma (6), Odontobarus (6)
Chyoromera, Heterendaeopsis
7
E
Nipponochyromera
Endaenidius (6)
1 2 3
Katsurazo
F
11
Latiphronus (6)
Heterimerodes (5)
Heterochyromera
H
8 9 10
12 13
Minyrus
Aedenus
Lepidimerodes (6)
B
G
14
Hexeria, Synnadophila
Nesendaeus, Gryporrhynchus (6)
Endaeus (6), Synnadichnus (6)
Eugryporrhynchus (5), Agryporrhynchus



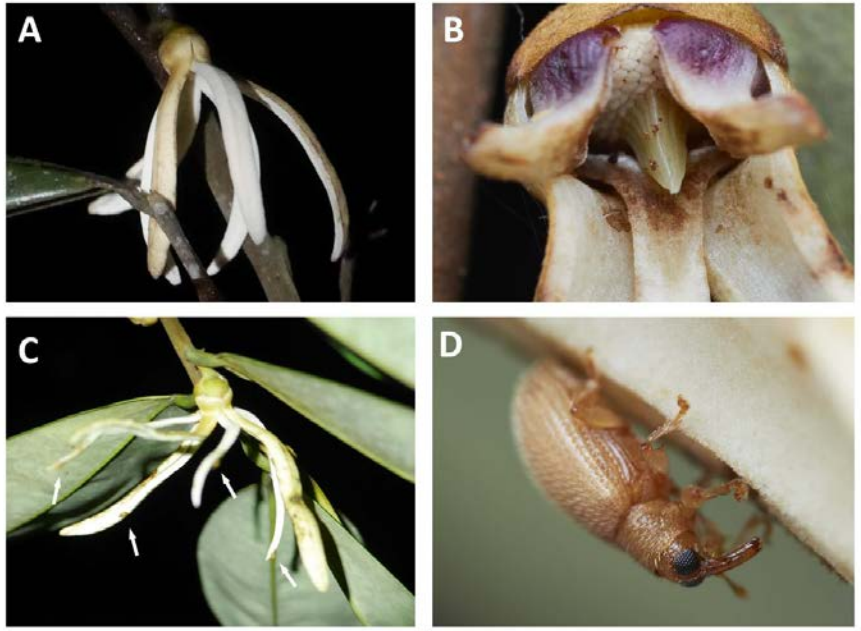
Endaeus xylopiae Haran & Zelvelder



Endaeus jaculifer Haran & Zelvelder

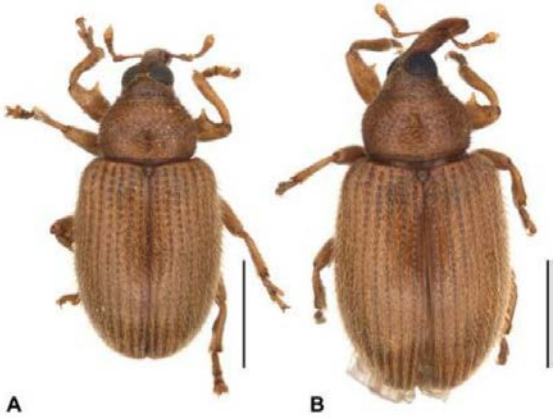


Endaeus convexiculus Haran & Zelvelder

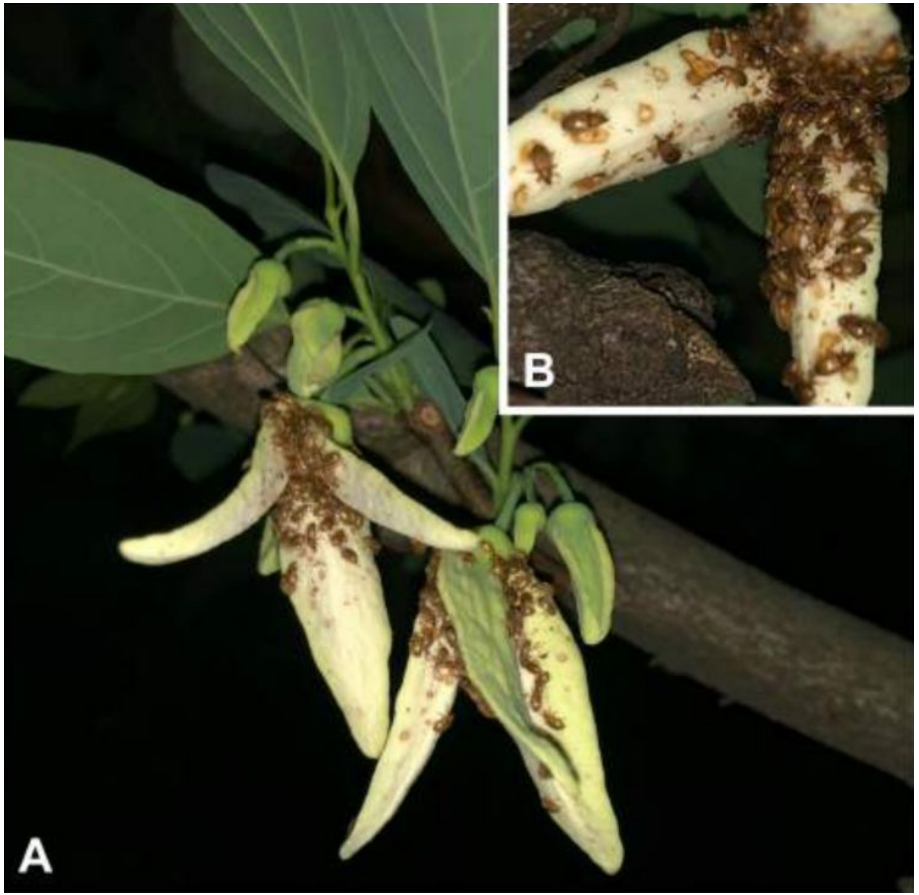


Xylopia aethiopica (Dunal) A.Rich.

Haran et al. 2026



Endaeus inexpectatus Hsiao & Kojima

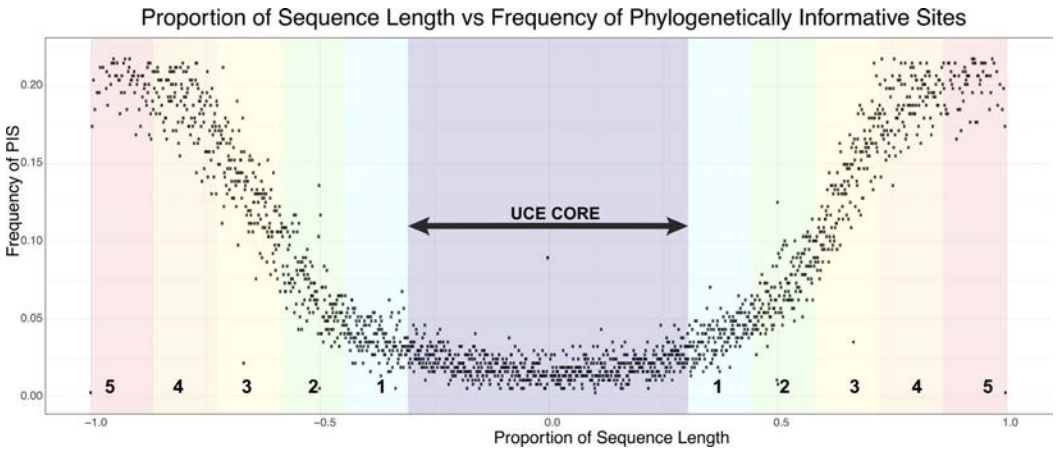


Annona squamosa (introduced in Vietnam)

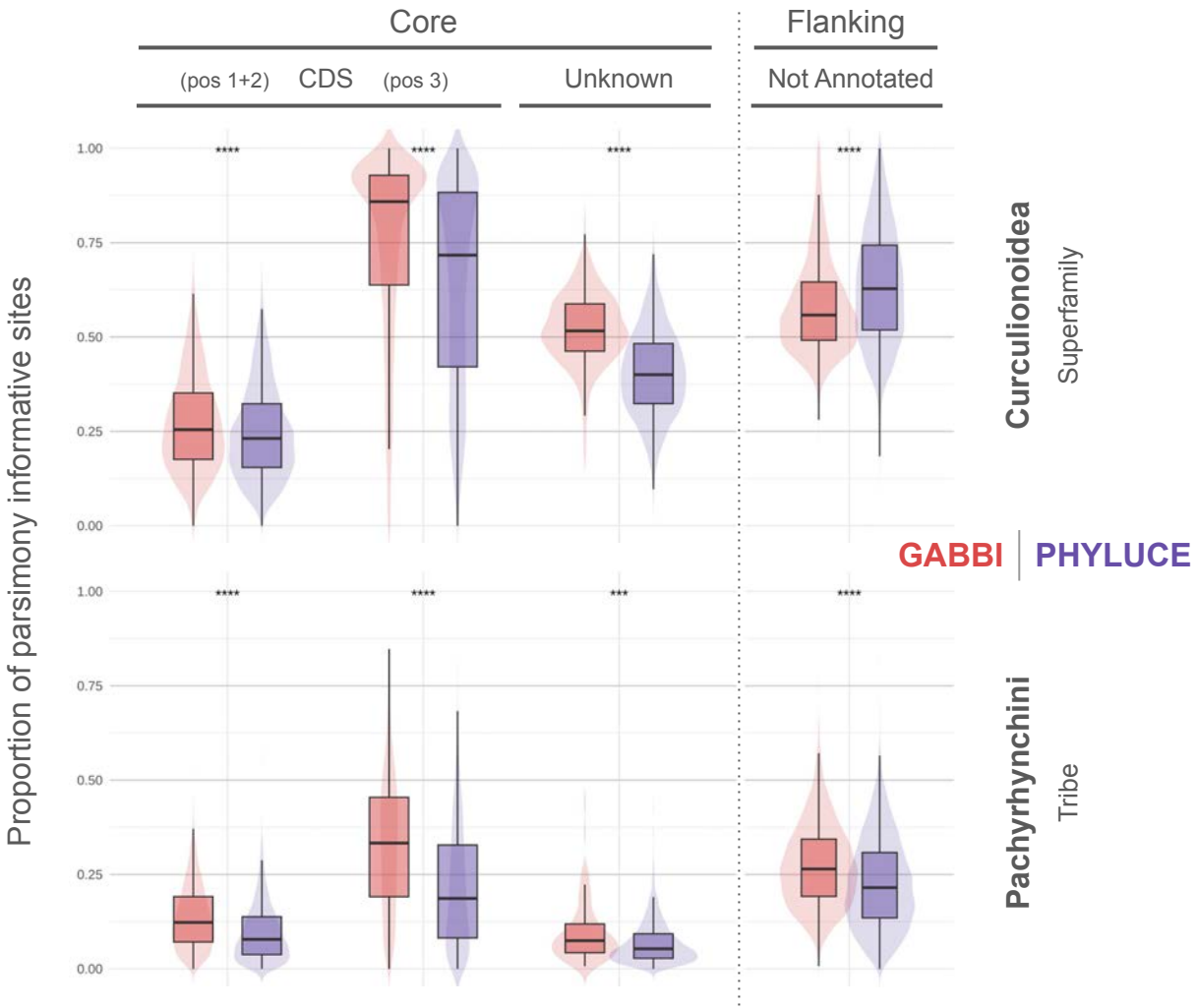
Hsiao et al. 2025

Short
degraded DNA

Long
unfragmented DNA

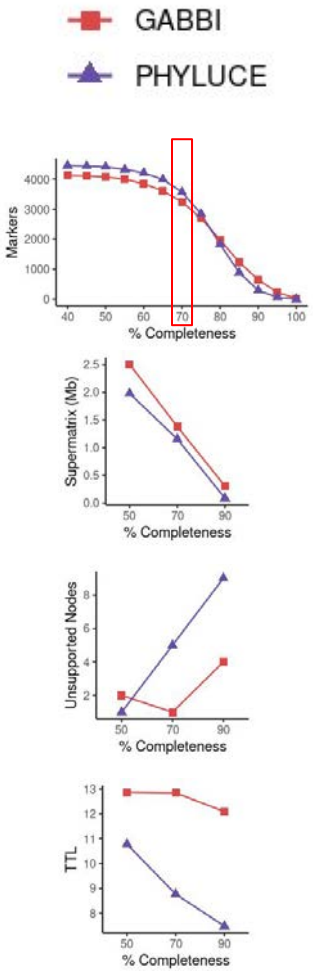


Van Dam et al. 2017



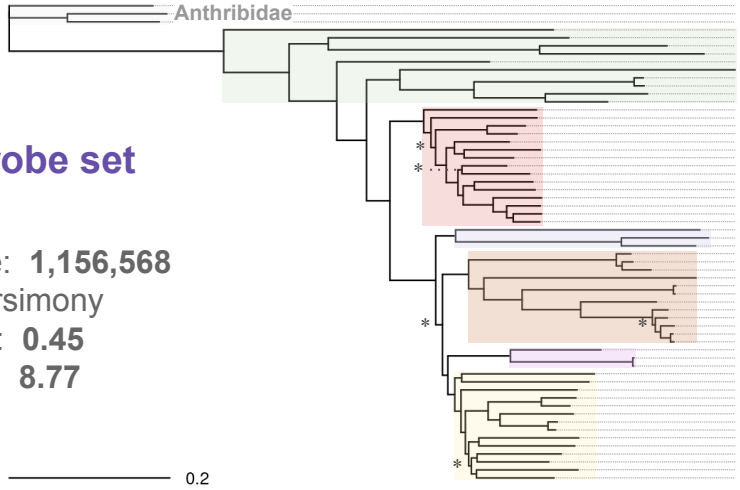
Zelvelder et al. 2026 (preprint)

Superfamily Curculionoidea



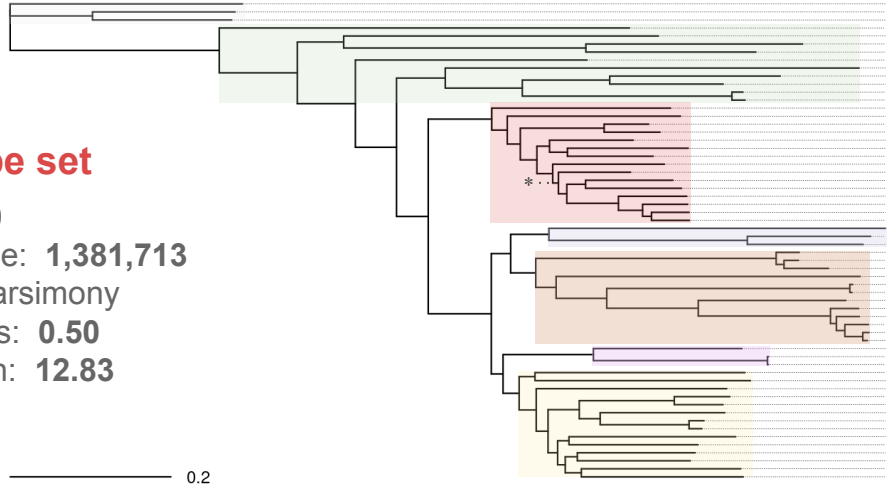
PHYLUCE probe set

Markers: **3,568**
Supermatrix size: **1,156,568**
Proportion of parsimony informative sites: **0.45**
Total tree length: **8.77**



GABBI probe set

Markers: **3,239**
Supermatrix size: **1,381,713**
Proportion of parsimony informative sites: **0.50**
Total tree length: **12.83**



'Early diverging lineages'

CEGH

Curculioninae II

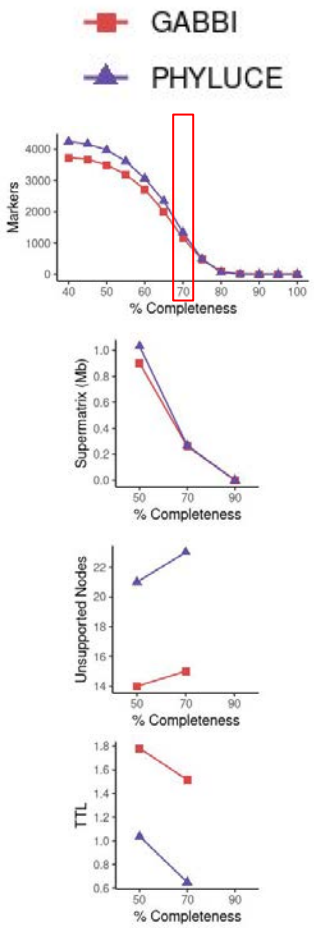
Scolytinae

Ceutorhynchinae

Curculioninae I + Molytinae

Zelvelder et al. 2026 (preprint)

Tribe Pachyrhynchini

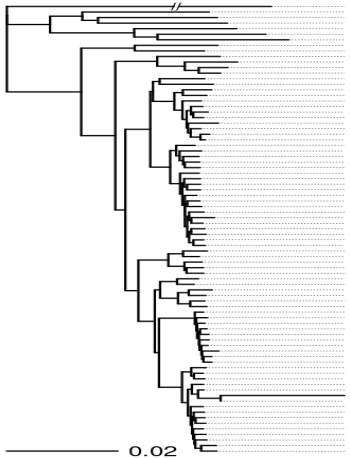


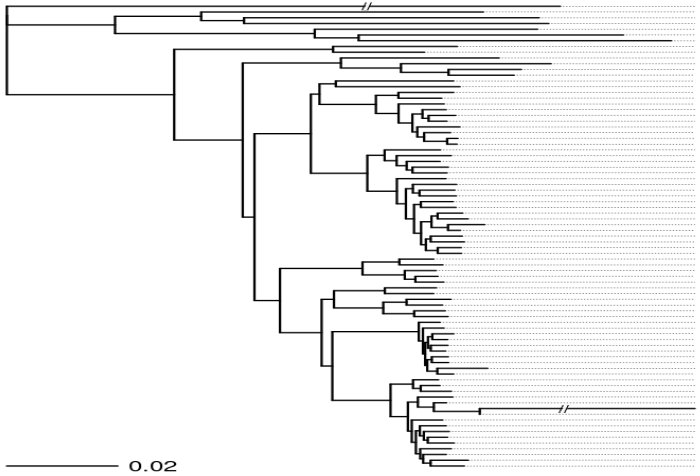
PHYLUCE probe set

Markers: **1,335**
Supermatrix size: **266,716**
Proportion of parsimony informative sites: **0.10**
Total tree length: **0.65**

GABBI probe set

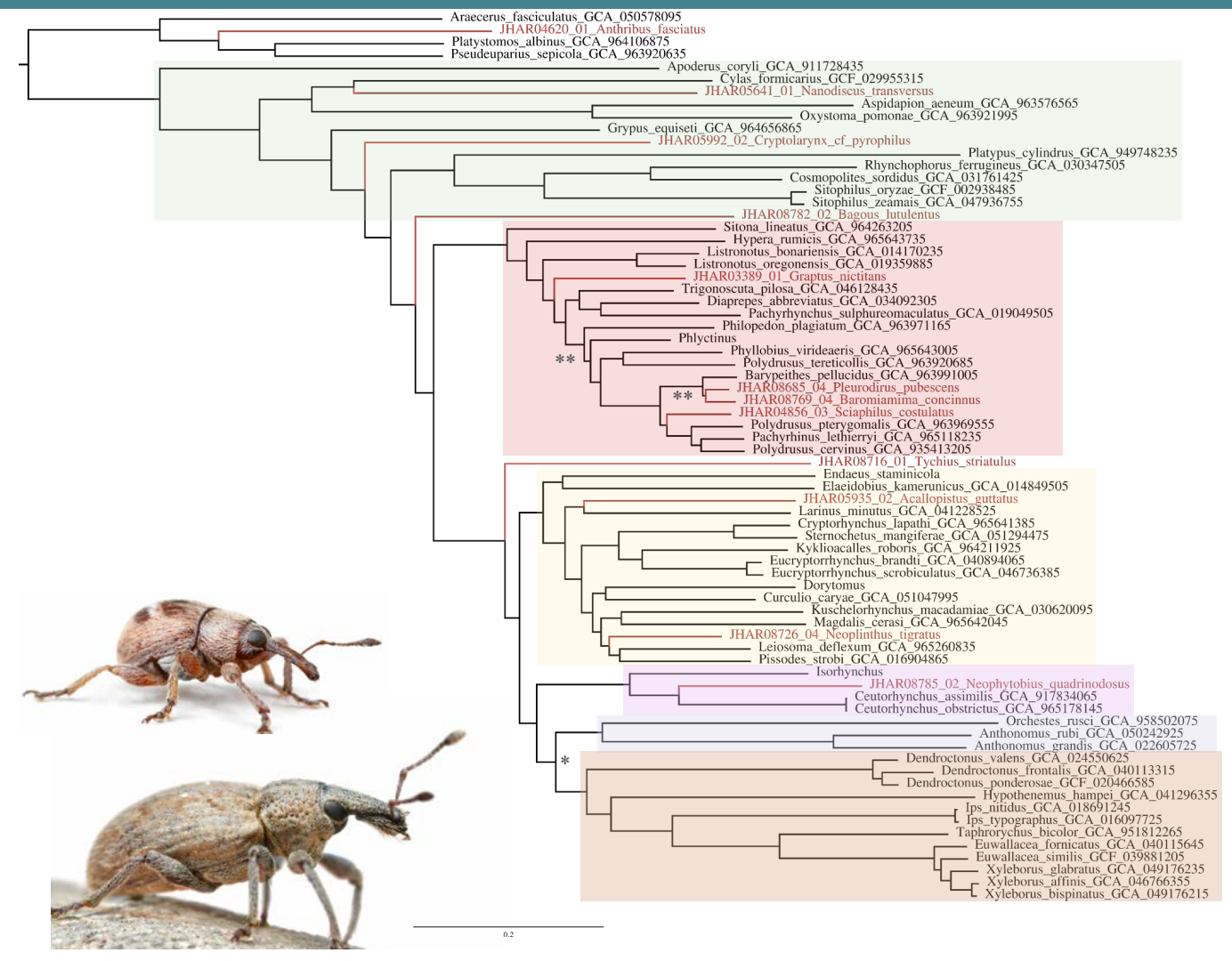
Markers: **1,161**
Supermatrix size: **261,147**
Proportion of parsimony informative sites: **0.20**
Total tree length: **1.51**



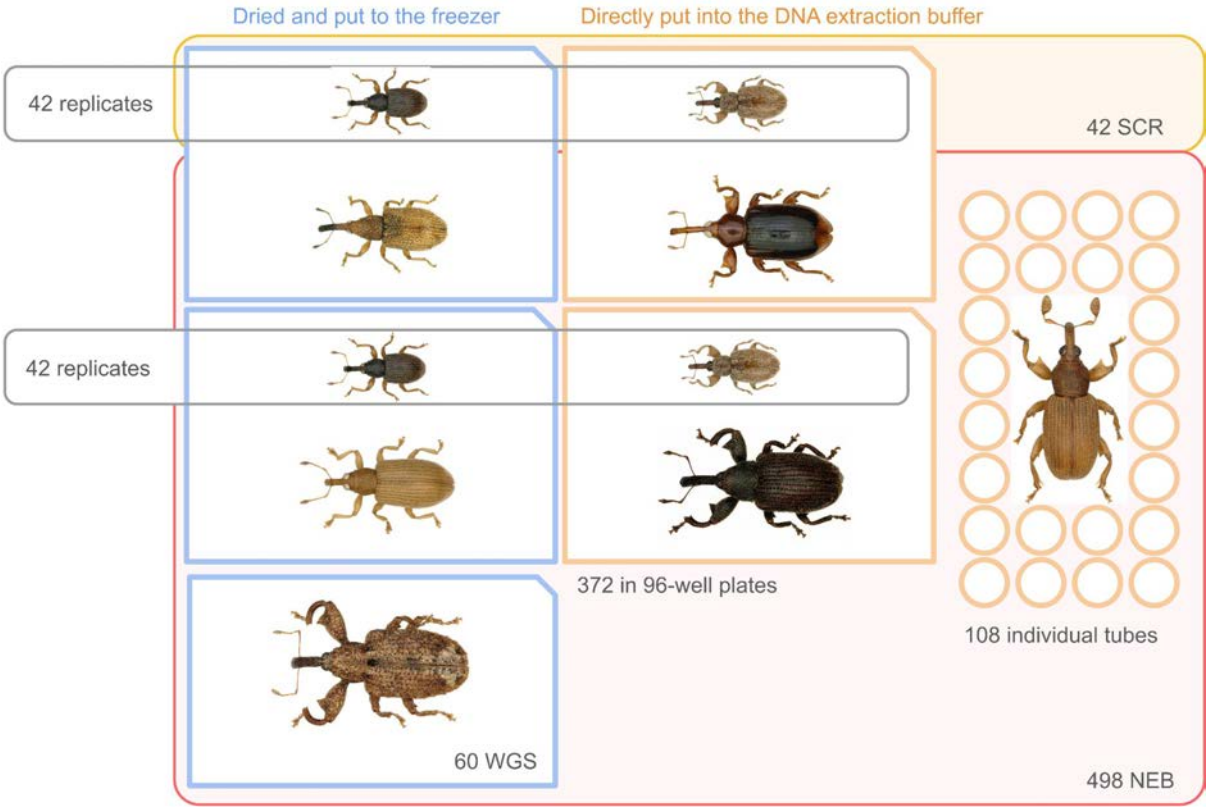


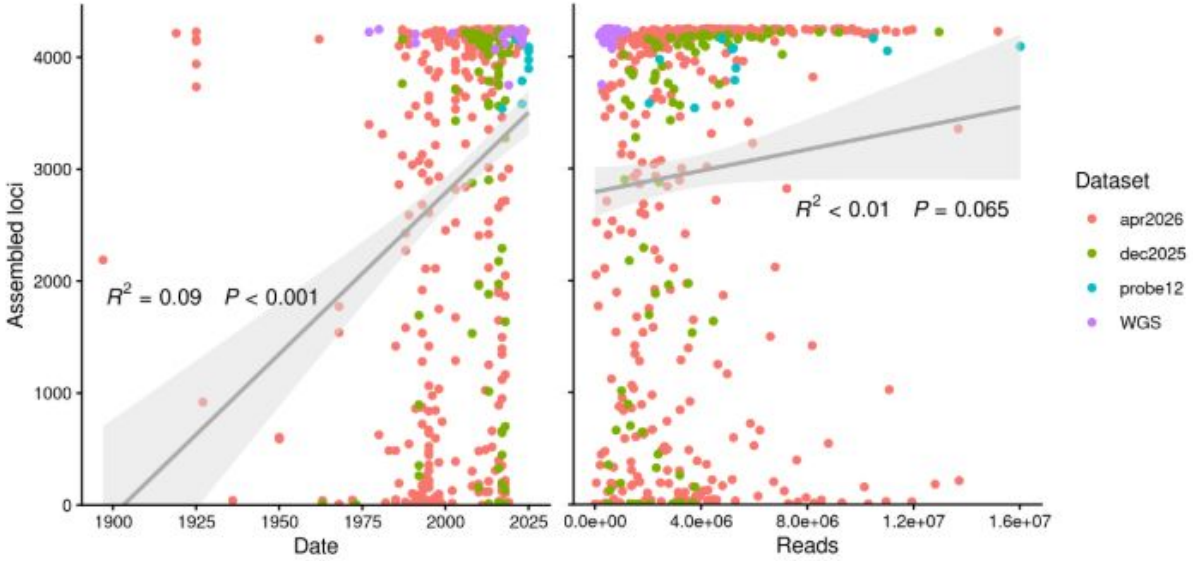
data from Van Dam et al. 2023, Syst. Bio.

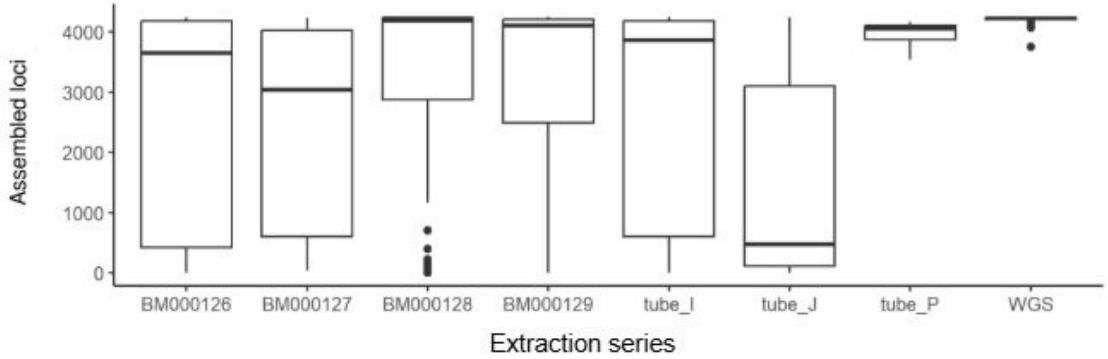
Zelvelder et al. 2026 (preprint)

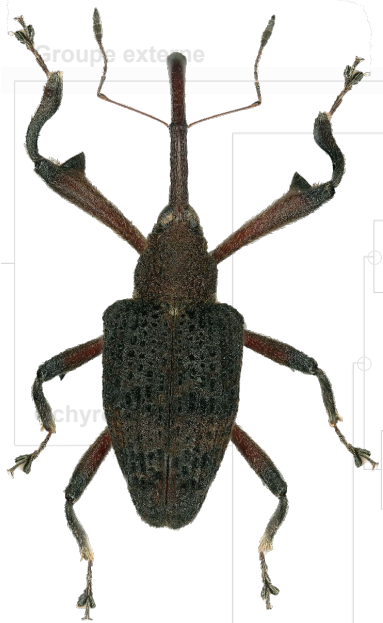


Zelvelder et al. 2026 (preprint)


Dried and put to the freezer
Directly put into the DNA extraction buffer
42 replicates
42 replicates
42 SCR
372 in 96-well plates
108 individual tubes
60 WGS
498 NEB


Assembled loci
4000
3000
2000
1000
0
R^2 = 0.09 P < 0.001
1900
1925
1950
1975
2000
2025
Date
R^2 < 0.01 P = 0.065
0.0e+00
4.0e+06
8.0e+06
1.2e+07
1.6e+07
Reads
Dataset
apr2026
dec2025
probe12
WGS


Assembled loci
4000
3000
2000
1000
0
BM000126
BM000127
BM000128
BM000129
tube_I
tube_J
tube_P
WGS
Extraction series



Drepanoscelus

Marshall 1938

- Antagoniste suspecté
- Antagoniste attesté
- Mutualiste suspecté
- Mutualiste attesté
- UFBS < 95
- SH-aLRT < 80 & UFBS < 95

Tychius
Synnadophila
cf. Hexeria gr. sp. 2
Nesendaeus n. sp. 2
Hexeria
Heterendaeus
Ochyromera gr. *hiramatsui*
Ochyromera gr. *hirokawai*
Ochyromera gr. sp. 108
Ochyromera gr. n. sp. 1
Parendaeus
Ochyromera gr. sp. 79
Ochyromera gr. sp. 126
Ochyromera gr. sp. 60
Nipponochyromera gr. sp. 2
Ochyromera gr. n. sp. 6
Opseoscapha
*Agryporrhynchus**
Ochyromera gr. *rufescens*
Ochyromera gr. *japonica*
Endaenidius sp. 12
Drepanoscelus
Eusynnada
Chyoromera
Eugryporrhynchus
Heterochyromera
Minyrus
Lepidimerodes
Aedenus
cf. *Aedenus* sp. 1
Katsurazo
*Agryporrhynchus** gr. n. sp. 2
Morimotozo

Chyroromera

Watanabe et al. 2017, 2018

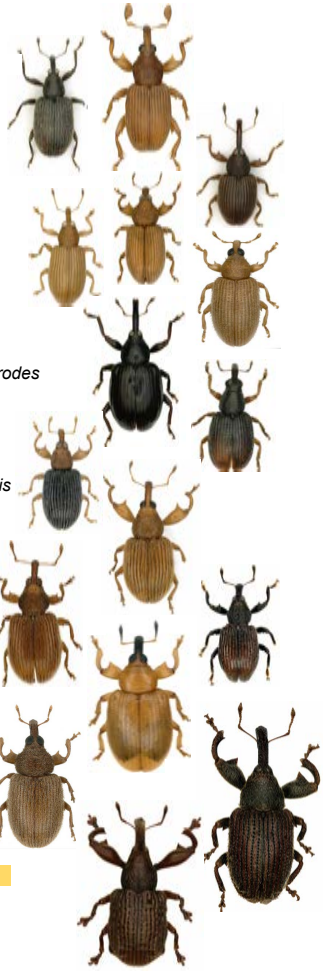
Groupe externe

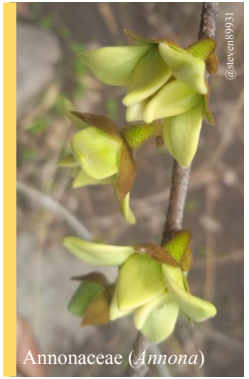
Tychius
Synnadophila
cf. Hexeria gr. sp. 2
Nesendaeus n. sp. 2
Hexeria
Heterendaeus
Ochyromera gr. *hiramatsui*
Ochyromera gr. *hirokawai*
Ochyromera gr. sp. 108
Ochyromera gr. n. sp. 1
Parendaeus
Ochyromera gr. sp. 79
Ochyromera gr. sp. 126
Ochyromera gr. sp. 60
Nipponochyromera gr. sp. 2
Ochyromera gr. n. sp. 6
Opseoscapha
*Agryporrhynchus**
Ochyromera gr. *rufescens*
Ochyromera gr. *japonica*
Endaenidius sp. 12
Drepanoscelus
Eusynnada
Chyoromera
Eugryporrhynchus
Heterochyromera
Minyrus
Lepidimerodes
Aedenus
cf. *Aedenus* sp. 1
Katsurazo
*Agryporrhynchus** gr. n. sp. 2
Morimotozo

- Antagoniste suspecté
- Antagoniste attesté
- Mutualiste suspecté
- Mutualiste attesté
- UFBS < 95
- SH-aLRT < 80 & UFBS < 95

Synnada

cf. *Aedenus* sp. 1
Katsurazo
*Agryporrhynchus** gr. n. sp. 2
Morimotozo
Synnadichnus
Endaenidius gr. *maetoi*
*Nychiomma**
Endaenidius gr. *ikezakii*
Endaenidius sp. 10
Endaeus gr. *canangae*
Endaenidius sp. 17
Heterimerodes
Adelus
*Synnada** gr. sp. 26
*Synnada** gr. sp. 30
*Synnada** cf. *flavoapicalis*
*Synnada** gr. sp. 45
*Synnada** gr. sp. 3
*Synnada** sp. 24
Endaeus gr. sp. 124
Endaeus gr. sp. 67
Endaeus gr. sp. 243
Endaeus gr. setulosus
Eutecheus
Endaeus gr. sp. 73
Endaeus gr. *lenticulatus*
Teinomphasus
Endaeus gr. *xylopiae*
Endaeus gr. *castus*
Endaeus gr. *floralis*
Omphasus
Endaeus gr. sp. 47
Endaeus gr. *bauhiniae*
Daeneus
Endaeus gr. sp. 64

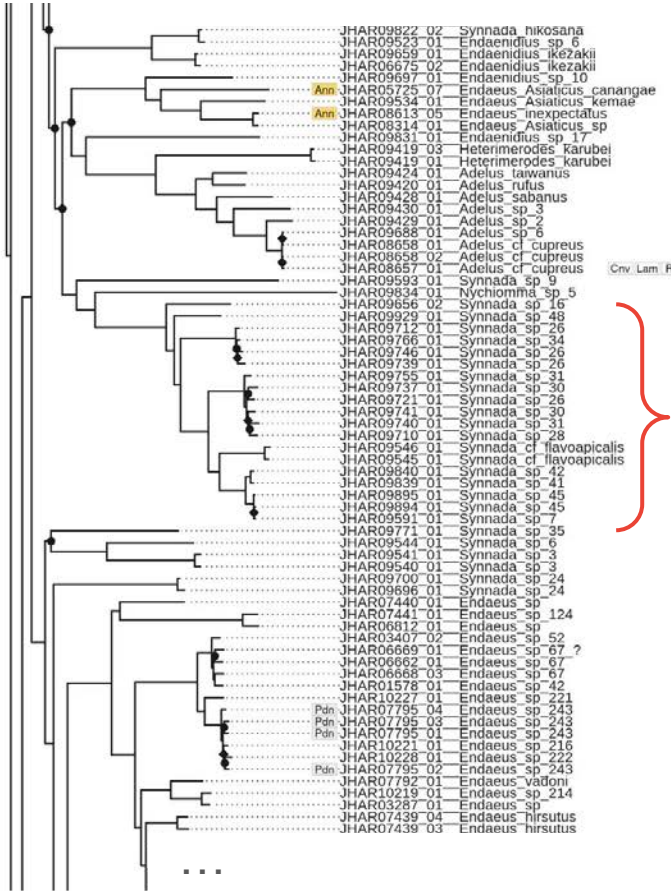


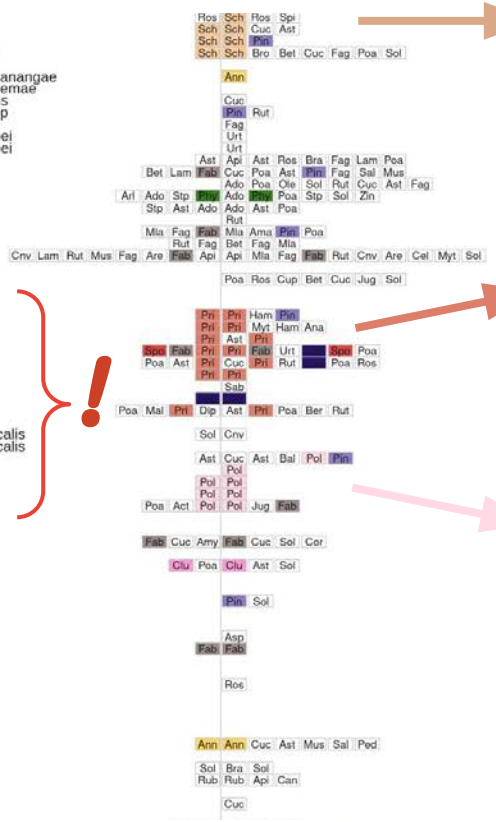


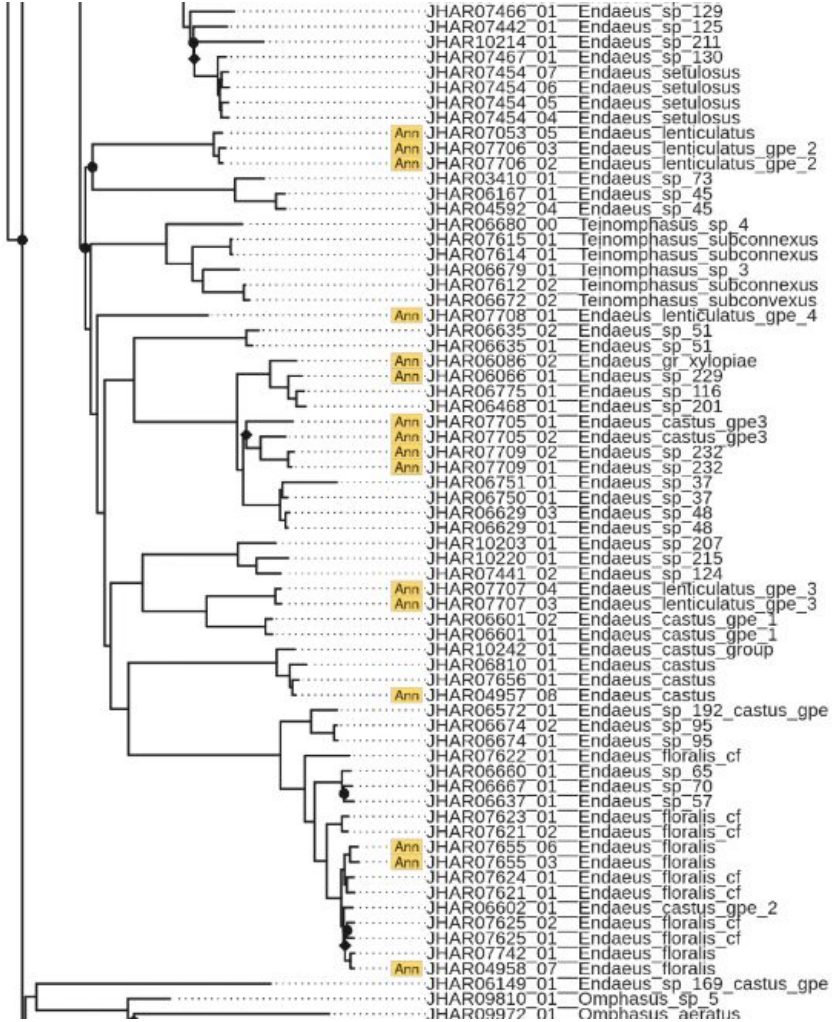
- Antagoniste suspecté
- Antagoniste attesté
- Mutualiste suspecté
- Mutualiste attesté
- UFBS < 95
- SH-aLRT < 80 & UFBS < 95

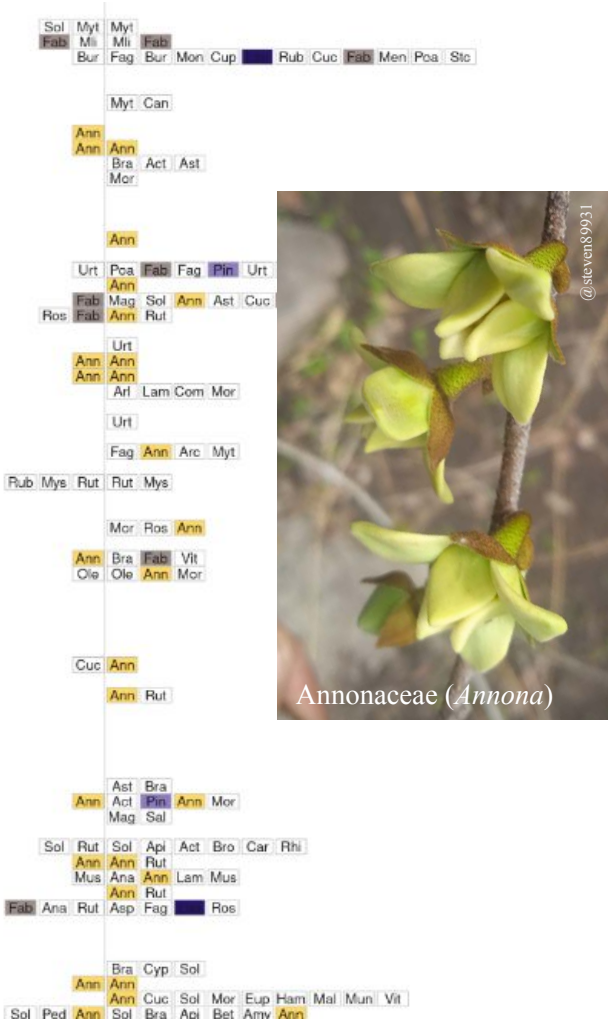
Plant sequences : matK | rbcL

Synnada






JHAR07466_01__Endaeus_sp_129
JHAR07442_01__Endaeus_sp_125
JHAR10214_01__Endaeus_sp_211
JHAR07467_01__Endaeus_sp_130
JHAR07454_07__Endaeus_setulosus
JHAR07454_06__Endaeus_setulosus
JHAR07454_05__Endaeus_setulosus
JHAR07454_04__Endaeus_setulosus
Ann JHAR07053_05__Endaeus_lenticulatus
Ann JHAR07706_03__Endaeus_lenticulatus_gpe_2
Ann JHAR07706_02__Endaeus_lenticulatus_gpe_2
JHAR03410_01__Endaeus_sp_73
JHAR06167_01__Endaeus_sp_45
JHAR04592_04__Endaeus_sp_45
JHAR06680_00__Teinomphasus_sp_4
JHAR07615_01__Teinomphasus_subconnexus
JHAR07614_01__Teinomphasus_subconnexus
JHAR06679_01__Teinomphasus_sp_3
JHAR07612_02__Teinomphasus_subconnexus
JHAR06672_02__Teinomphasus_subconvexus
Ann JHAR07708_01__Endaeus_lenticulatus_gpe_4
JHAR06635_02__Endaeus_sp_51
JHAR06635_01__Endaeus_sp_51
Ann JHAR06086_02__Endaeus_gr_xylopiae
Ann JHAR06066_01__Endaeus_sp_229
JHAR06775_01__Endaeus_sp_116
JHAR06468_01__Endaeus_sp_201
Ann JHAR07705_01__Endaeus_castus_gpe3
Ann JHAR07705_02__Endaeus_castus_gpe3
Ann JHAR07709_02__Endaeus_sp_232
Ann JHAR07709_01__Endaeus_sp_232
JHAR06751_01__Endaeus_sp_37
JHAR06750_01__Endaeus_sp_37
JHAR06629_03__Endaeus_sp_48
JHAR06629_01__Endaeus_sp_48
JHAR10203_01__Endaeus_sp_207
JHAR10220_01__Endaeus_sp_215
JHAR07441_02__Endaeus_sp_124
Ann JHAR07707_04__Endaeus_lenticulatus_gpe_3
Ann JHAR07707_03__Endaeus_lenticulatus_gpe_3
JHAR06601_02__Endaeus_castus_gpe_1
JHAR06601_01__Endaeus_castus_gpe_1
JHAR10242_01__Endaeus_castus_group
JHAR06810_01__Endaeus_castus
JHAR07656_01__Endaeus_castus
Ann JHAR04957_08__Endaeus_castus
JHAR06572_01__Endaeus_sp_192_castus_gpe
JHAR06674_02__Endaeus_sp_95
JHAR06674_01__Endaeus_sp_95
JHAR07622_01__Endaeus_floralis_cf
JHAR06660_01__Endaeus_sp_65
JHAR06667_01__Endaeus_sp_70
JHAR06637_01__Endaeus_sp_57
JHAR07623_01__Endaeus_floralis_cf
JHAR07621_02__Endaeus_floralis_cf
Ann JHAR07655_06__Endaeus_floralis
Ann JHAR07655_03__Endaeus_floralis
JHAR07624_01__Endaeus_floralis_cf
JHAR07621_01__Endaeus_floralis_cf
JHAR06602_01__Endaeus_castus_gpe_2
JHAR07625_02__Endaeus_floralis_cf
JHAR07625_01__Endaeus_floralis_cf
JHAR07742_01__Endaeus_floralis
Ann JHAR04958_07__Endaeus_floralis
JHAR06149_01__Endaeus_sp_169_castus_gpe
JHAR09810_01__Omphasus_sp_5
JHAR09972_01__Omphasus_aeratus


Annonaceae (*Annona*)
@steven89931

cf. Eudela castanea Lea

Endaeus castus Schoenherr