Molecular and morphological phylogenies in insects – controversial or concordant? The sample from the geometroid lepidopterans (Lepidoptera: Geometriformes)

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1. Short introduction on the subject of my work

I study the geometroid lepidopterans, mainly - geometrid moths: their
- taxonomy, ecology, biogeography, but the focus of my interest – morphology and phylogeny of this group of families.

- Beljaev E.A. 1992. [Comparative analysis of phylogenetic and statistic methods on the sample of geometrids of the genera *Euchristophia* Fletch. and *Cabera* Tr. (Lepidoptera, Geometridae)]. *A.I. Kurentzov's Annual Memorial Meetings*. Iss. 3: 52-63.
- Beljaev E.A. 1997. A new genus and new species of the Ennominae (Lepidoptera, Geometridae) from Russian Far East, with remarks on the phylogeny of the related genera. *Tinea* 15 (2): 125–130.
- Beljaev E.A. 1998. [Morphology of the copulative apparatus of *Devenilia corearia* and description of the new tribe Deveniliini (Lepidoptera, Geometridae, Ennominae)]. *Zoologicheskij Zhurnal* 77 (4): 438–443.
- Beljaev E.A. 1998. A new genus of the Ennominae from East Asia, with notes on the phylogeny of some Holarctic Anagogoni (Lepidoptera, Geometridae). *Tinea* 15 (3): 266–270.
- Beljaev E.A. 2000. Remarkable new genus and new species of the geometrid moths from Central Asia, related to the genus Desertobia Viidallepp, 1989 (Lepidoptera, Geometridae, Ennominae) with notes on the taxonomy of the Desertobiini. *Tinea* 16 (4): 240–245.
- Beljaev E.A. 2003a. Phylogenetic significance of skeleton-muscular anatomy of the genitalia in Geometridae. *Spixiana – Zeitschrift fur Zoologie* 26 (3): 206–207.
- Beljaev E.A. 2003b. Notes to the molecular phylogeny of the Geometridae. *Spixiana – Zeitschrift fur Zoologie* 26 (3): 208.
- Beljaev E.A. 2006. A morphological approach to the Ennominae phylogeny (Lepidoptera, Geometridae). *Spixiana – Zeitschrift fur Zoologie* 29(3): 215–216.
- Beljaev E.A. 2007. Taxonomic changes in the emerald moths (Lepidoptera: Geometridae, Geometrinae) of East Asia, with notes on the systematics and phylogeny of Hemitheini. *Zootaxa* 1584: 55–68.
- **Beljaev E.A. 2008a. [Phylogenetic relationships of the family Geometridae and its subfamilies]. *Meetings in memory of N. A. Cholodkovsky*. Iss. 60. St.-Petersburg. 238 p.**
- Beljaev E.A. 2008b. New concept of the generic composition of the tribe Ennomini (Lepidoptera: Geometridae) based on the functional morphology of the male genitalia. *Entomologicheskoe obothrenie* 87 (2): 152–165.
- Beljaev E.A. 2009a. Phylogenetic relationships of the geometroid lepidopterans (Lepidoptera: Cimeliidae, Epicopeiidae, Sematuridae, Drepanidae, Uraniidae, Geometridae). *Spixiana – Zeitschrift fur Zoologie* 32(1): 23–24.
- Beljaev E.A. 2009b. Phylogenetic position of the tribe Azelinini (Lepidoptera: Geometridae, Ennominae) based on functional morphology of the male genitalia. *Euroasian Entomological Journal* 8(2): 82–84.

2. Families of Geometriformes

Cimeliidae

Axia margarita Hübn.

Sematuridae

Sematura lunus L.

Epicopeiidae

Epicopeia mencia Moore

Drepanidae

Drepana acuta Butl.

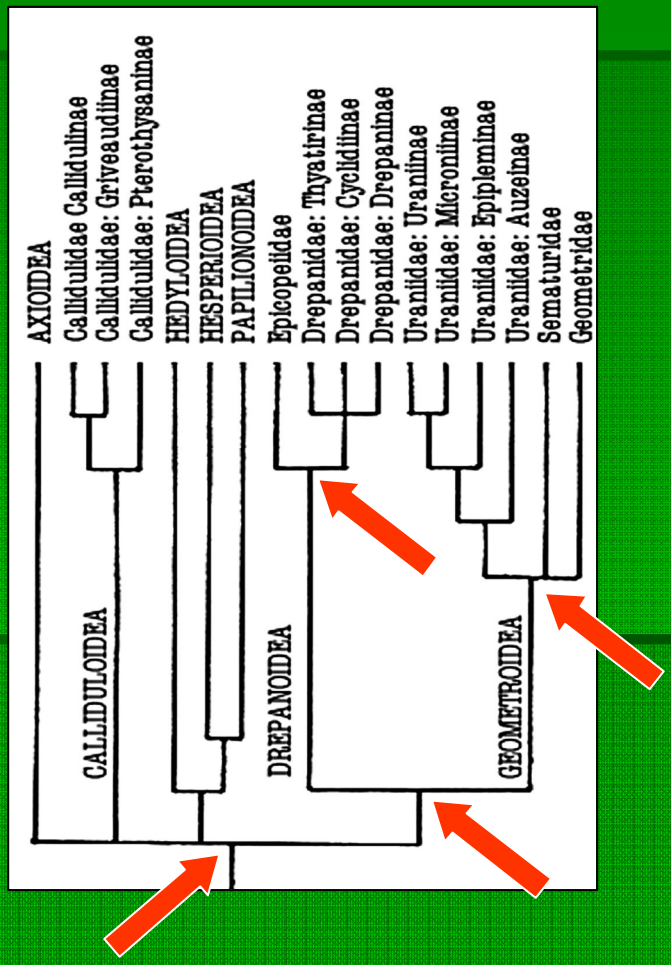
Uraniidae

Acropteris iphiata Guen.

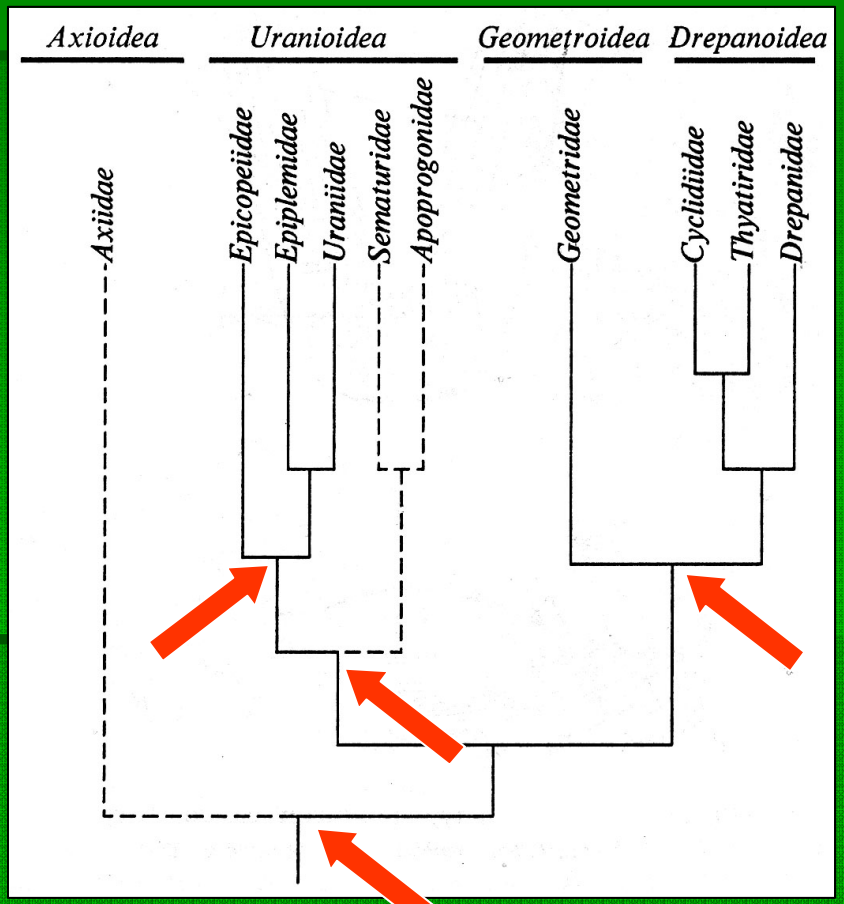
Geometridae

Geometra papilionaria L.

3. Previous recent morphological phylogenies of Geometriformes: a lot of contradictions

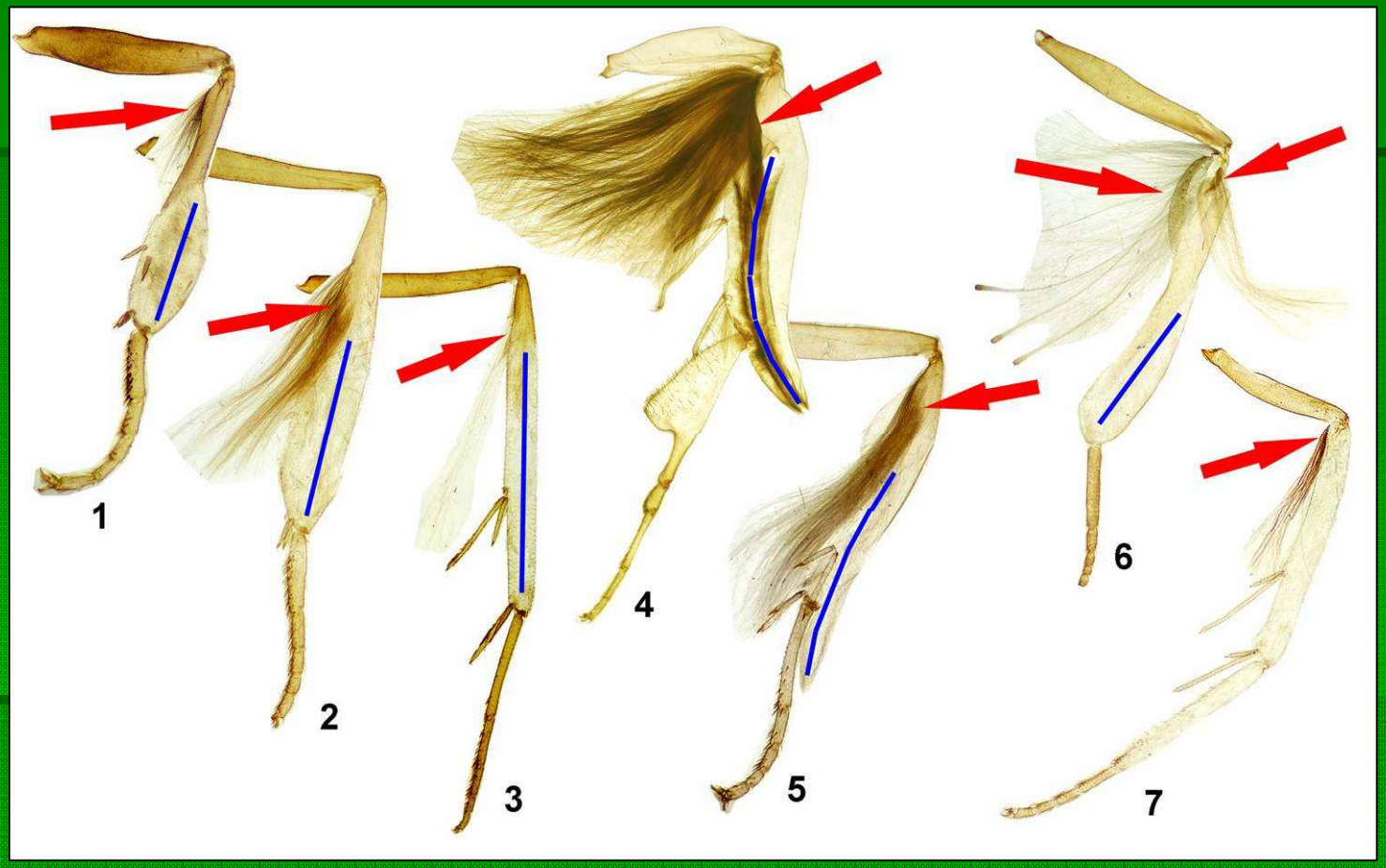


Holloway, 1998



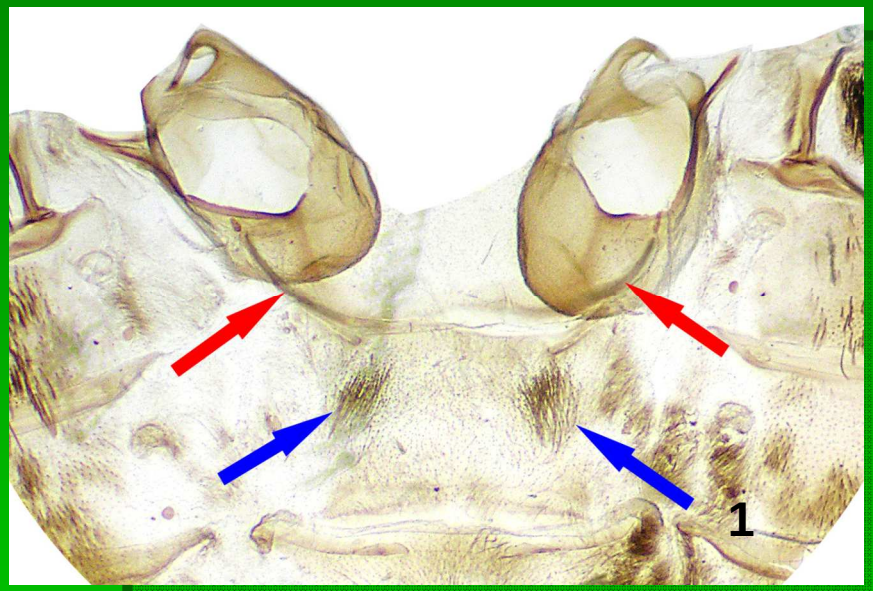
Kiznetzov, Stekolnikov, 2001

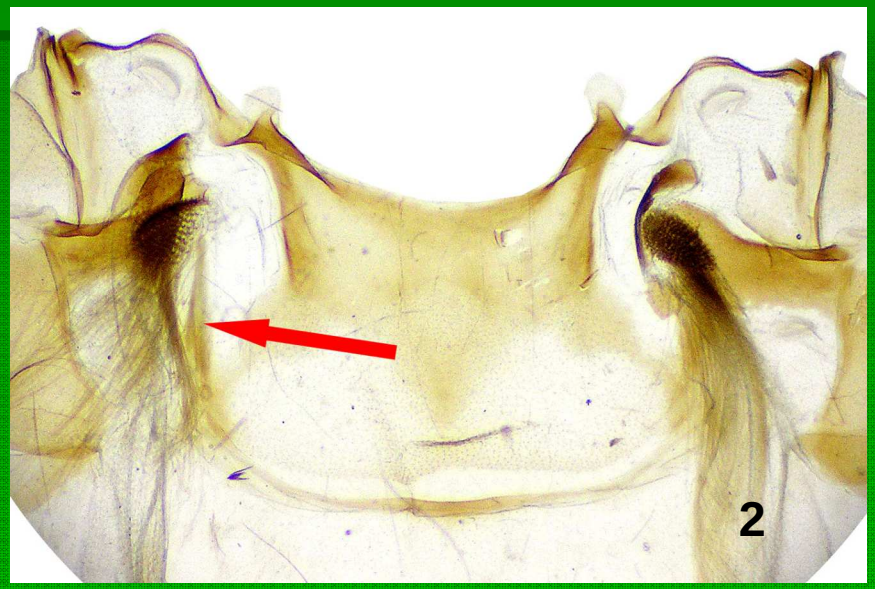
4. Tibial androconial apparatus of males in Geometridae



1 – Archiearinae (*Archiearis parthenias*); 2 – Ennominae (*Cystidia couaggaria*);
3 – Oenochrominae (*Epidesmia chilonaria*); 4 – Desmobathrinae (*Celerena signata*);
5 – Geometrinae (*Eucyclodes difficta*); 6 – Sterrhinae (*Problepsis phoebearia*);
7 – Larentiinae (*Lobophora halterata*).

5. Basal abdominal sternites in Geometriformes

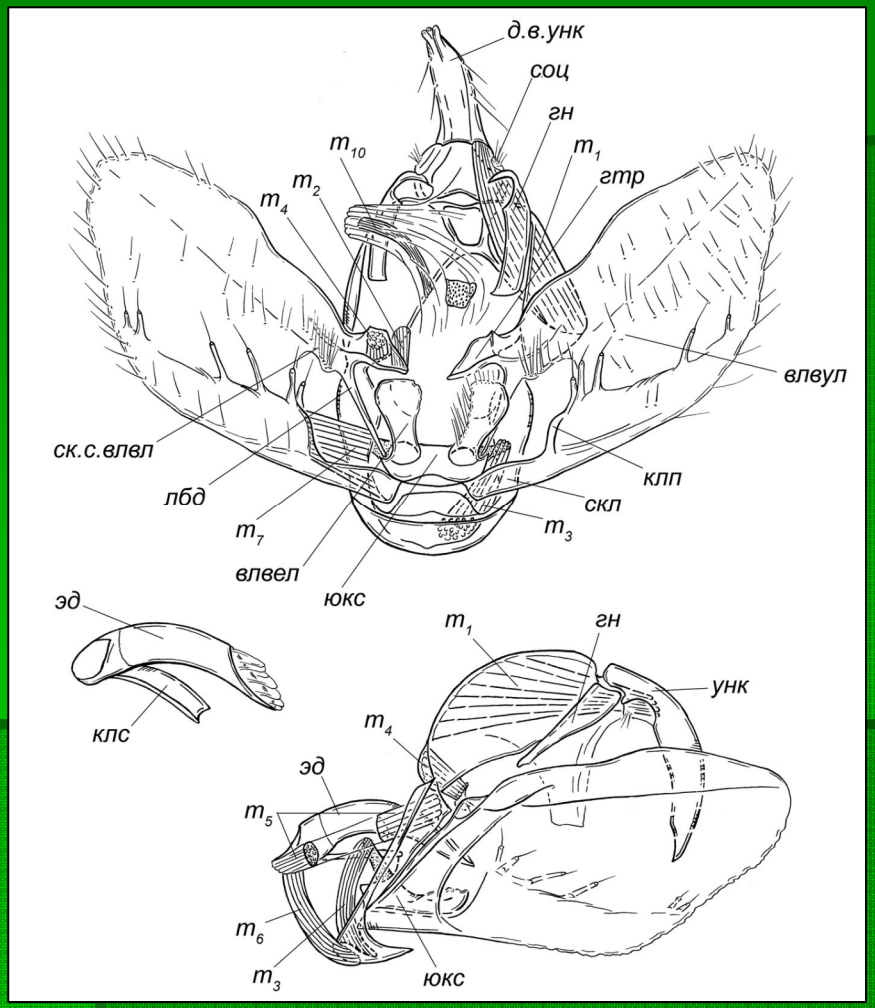




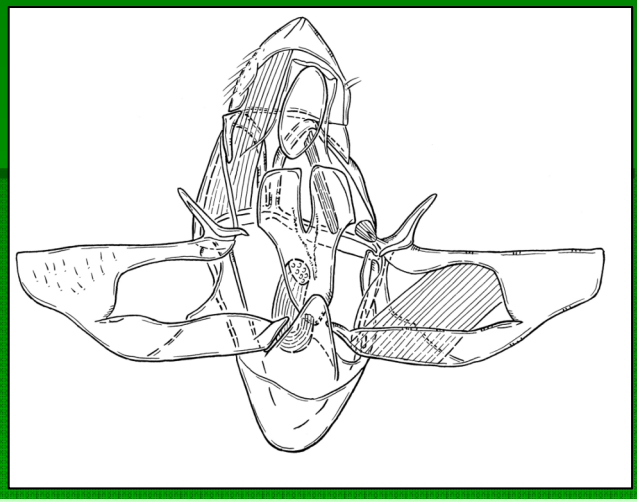
1 – Geometridae (*Archiearis notha*)

2 – Epicopeiidae (*Nossa palaearctica*)

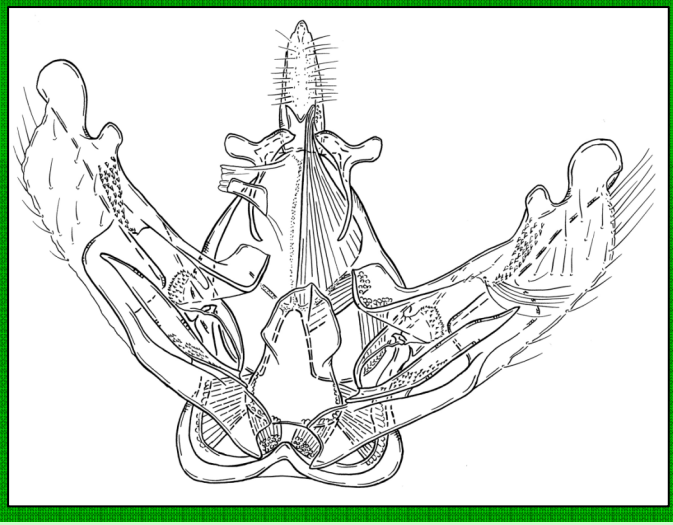
6. Skeleton-muscular structure of the male genitala



Sematuridae, *Sematura* sp.

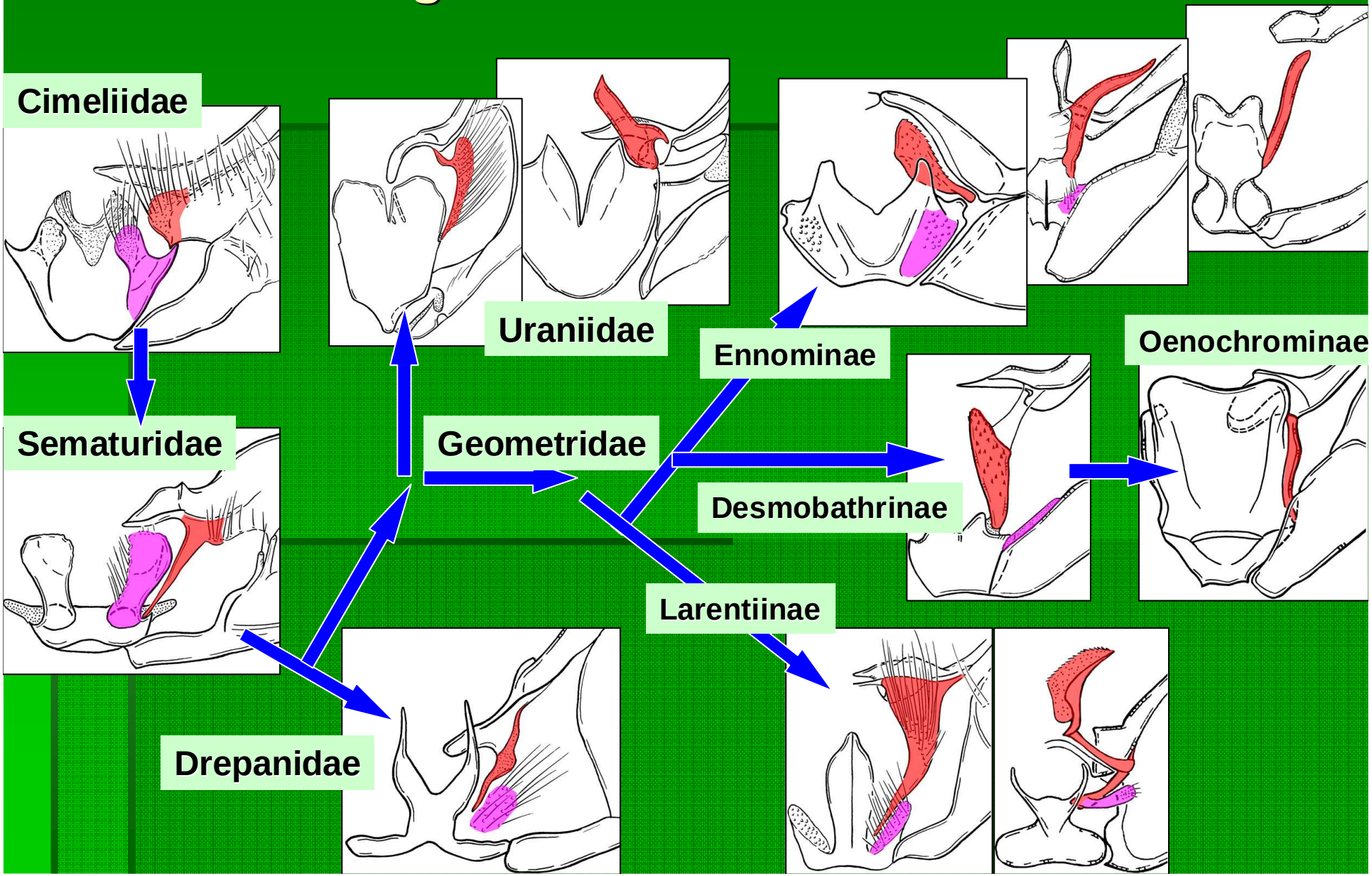


Geometridae, *Alsophila zabolne* Inoue



Geometridae, *Ozola sinuicosta* Prt.

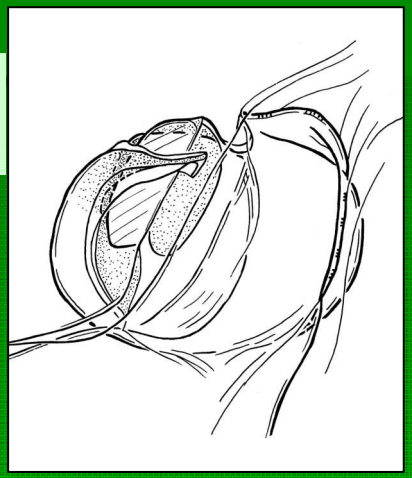
7. Transformations of labides and valvellae in the male genitalia of Geometriformes

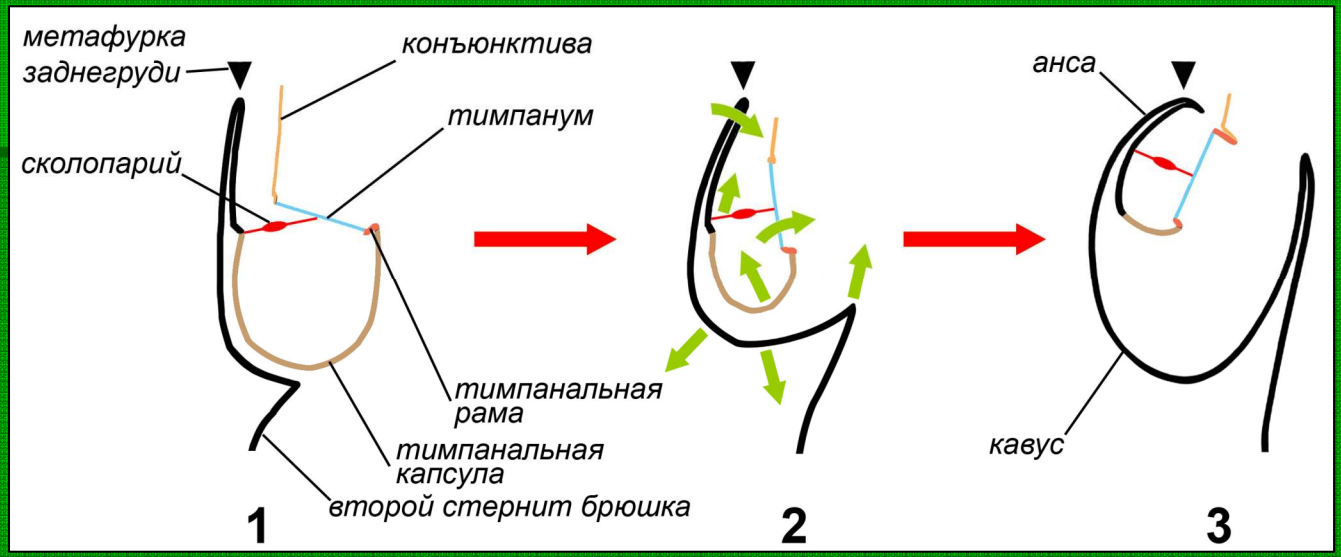


8. Hypothetic scheme of transformations of tympanal organ of uraniid-type into tympanal organ of geometrid-type

Uraniidae,
Lyssa zampa

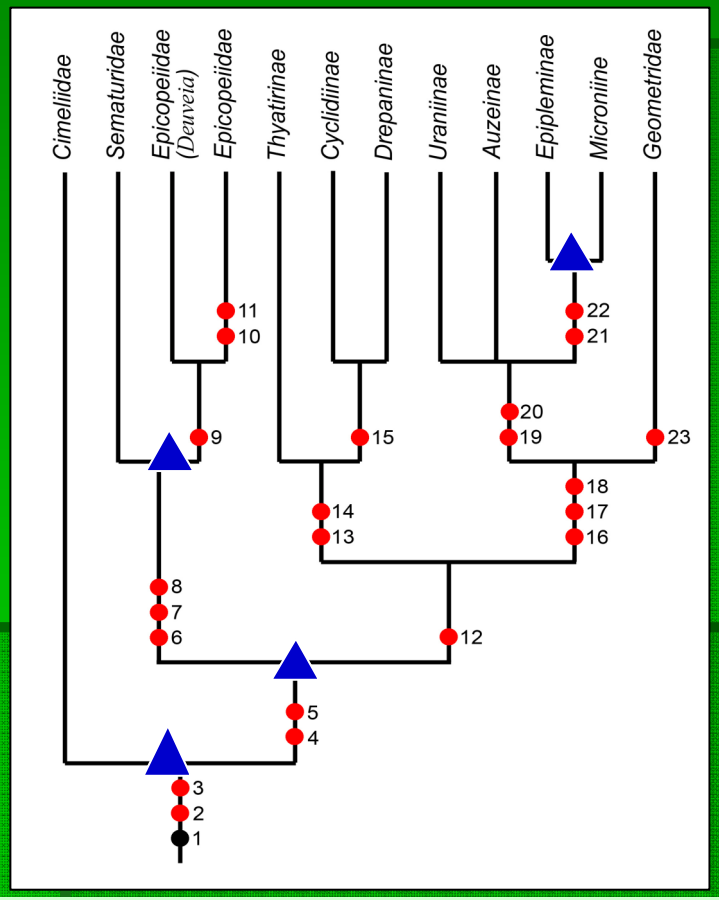
Geometridae,
***Monoctenia* sp.**



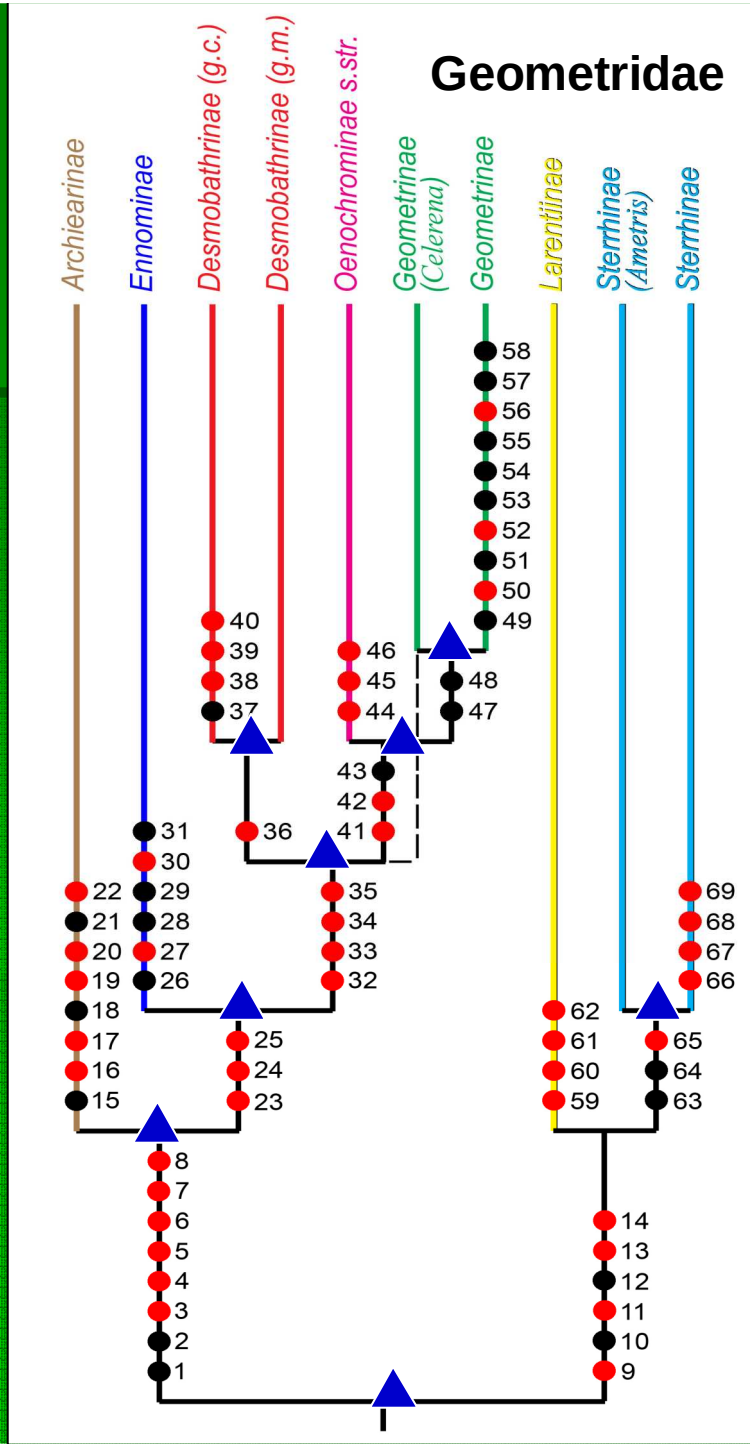


9. Original morphological phylogeny of the families and subfamilies of Geometriformes

(Beljaev, 2008)



- black circle - apomorphies after the different authors
- red circle - new apomorphies
- blue triangle - new nodes



10. Principles of reconstruction of the phylogeny

The principal theoretical point of my reconstruction of the phylogeny of Geometriformes – the statement, that

apomorphy - is not state of character but a fact that this state was obtained once.

This approach:

- do not allows take a character as it is, without the prior analyses of possible ways of its origin and transformation;
- it requires exacting selection of the characters fit for the search of the "phylogenic signal".
- is based on deep comparative-morphological analysis of material oriented on search of morphological homologies, construction of rows of morphological transformations and formulation of hypotheses about probable synapomorphies;
- supposes manual reconstruction of phylogeny because it based on a prior intensional analysis and it is not "objective", that is not formal in the character selection.

Principal question for testing of this approach:
how this phylogeny correlates with the modern molecular phylogenies in Lepidoptera?

11. Modern molecular phylogenies considering the geometrid lepidopterans

Geometridae:

- **Yamamoto**, S. & **Sota**, T. (**2007**) Phylogeny of the Geometridae and the evolution of winter moths inferred from a simultaneous analysis of mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 44: 711-723.

  - 75 species, 2.9 kb total bp

- **Sihvonen** P, Mutanen M, Kaila L, Brehm G, Hausmann A, et al. (**2011**) Comprehensive Molecular Sampling Yields a Robust Phylogeny for Geometrid Moths (Lepidoptera: Geometridae). *PLoS ONE* 6(6): e20356. doi:10.1371/journal.pone.0020356

  - 150 species, 6.2 kb total bp

Lepidoptera, including the families of Geometriformes:

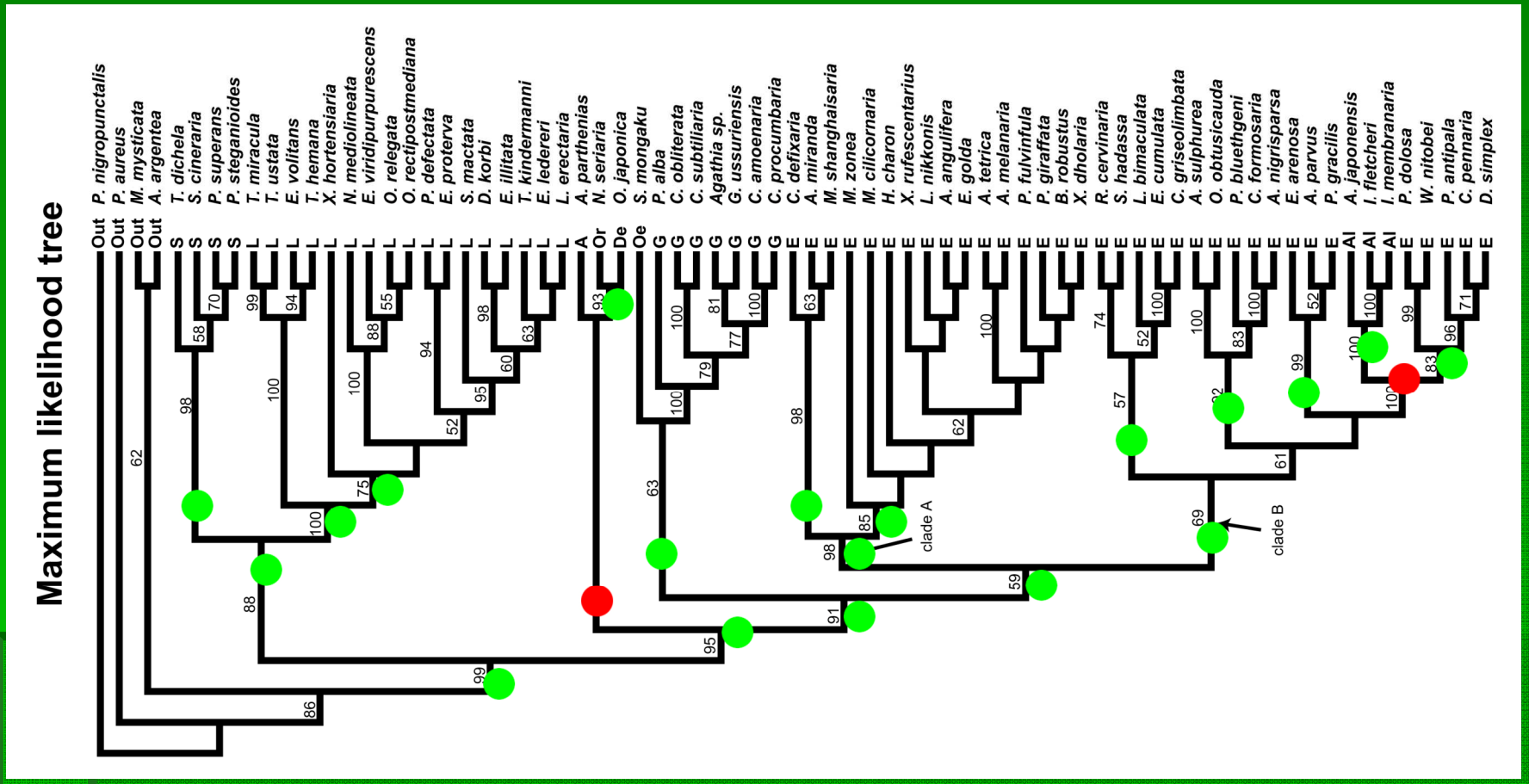
- **Regier**, J. C., Zwick, A., Cummings, M. P., Kawahara, A. Y., Cho, S., Weller, S., Roe, A., Baixeras, J., Brown, J. W., Parr, C., Davis, D. R., Epstein, M., Hallwachs, W., Hausmann, A., Janzen, D. H., Kitching, I. J., Solis, M. A., Yen, S.-H., Bazinet, A. L., Mitter, Ch. (**2009**) Toward reconstructing the evolution of advanced moths and butterflies (Lepidoptera: Ditrysia): an initial molecular study. *BMC Evolutionary Biology* 2009, 9: 280 doi:10.1186/1471-2148-9-280, 21 pp.

  - 123 species, 6.7 kb total bp

- **Mutanen** M., Wahlberg N. and Kaila L. (**2010**) Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings of the Royal Society B* (*Biological Sciences*). p 1-10. doi: 10.1098/rspb..0392.

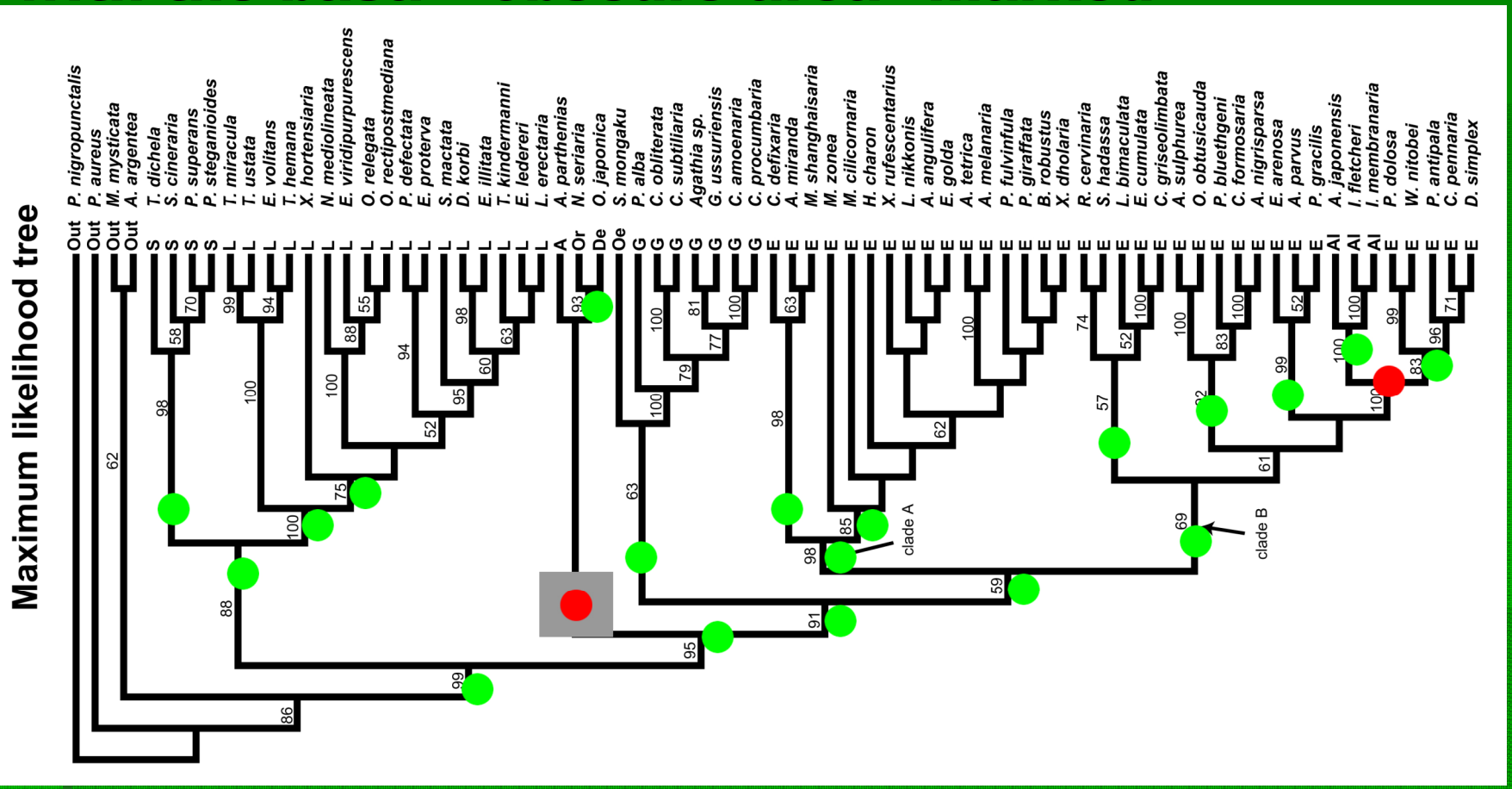
  - 350 species, 6.3 kb total bp

12. Yamamoto, Sota, 2007 – phylogenetic tree of Geometridae



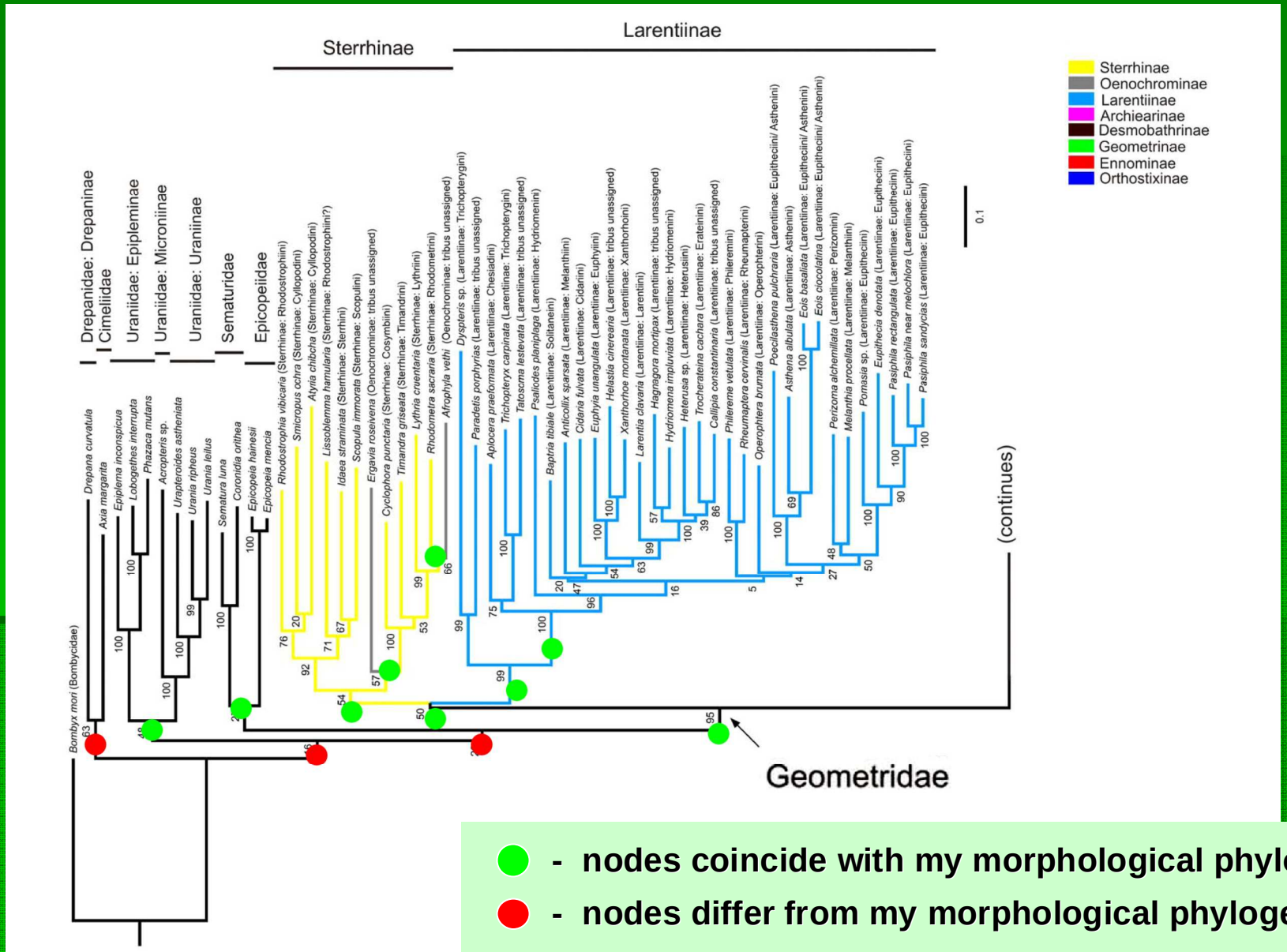
- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny

13. Yamamoto, Sota, 2007 – phylogenetic tree of Geometridae with the basal “obscure area” marked



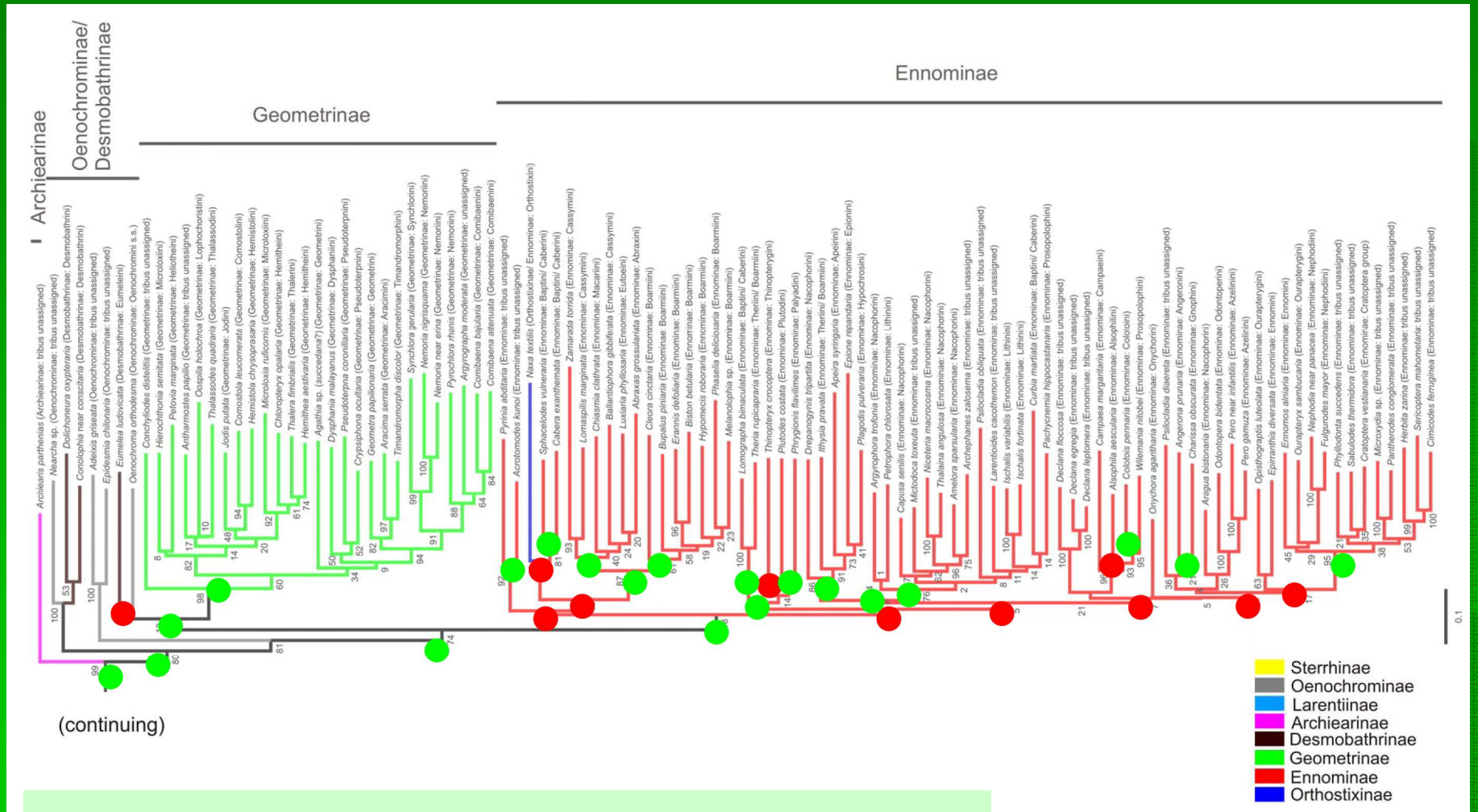
- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny
- “obscure area” – nodes with bootstrap value < 50

14. Sihvonen et al., 2011 – phylogenetic tree of Geometridae, first portion



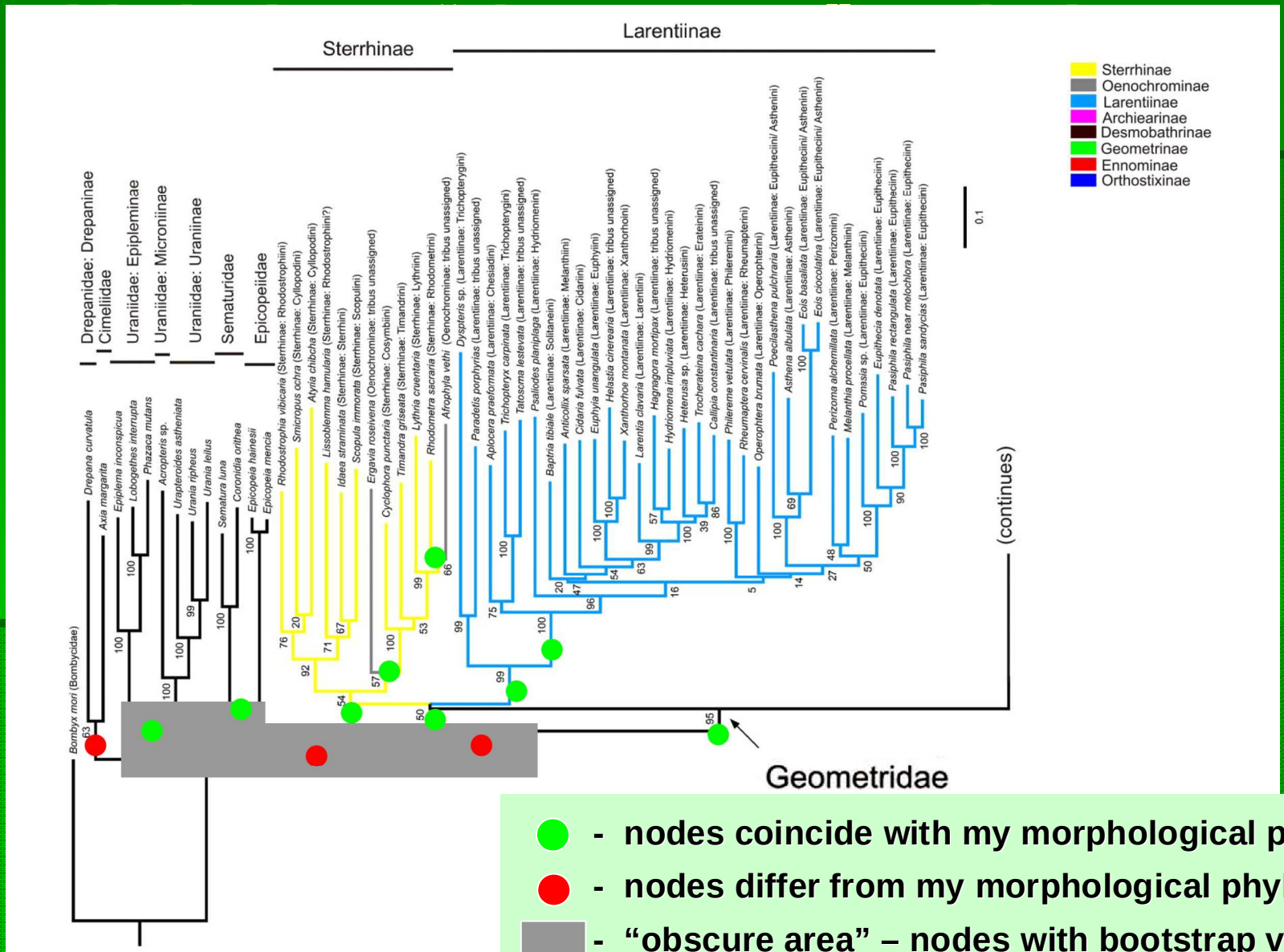
- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny

15. Sihvonen et al., 2011 – phylogenetic tree of Geometridae, second portion



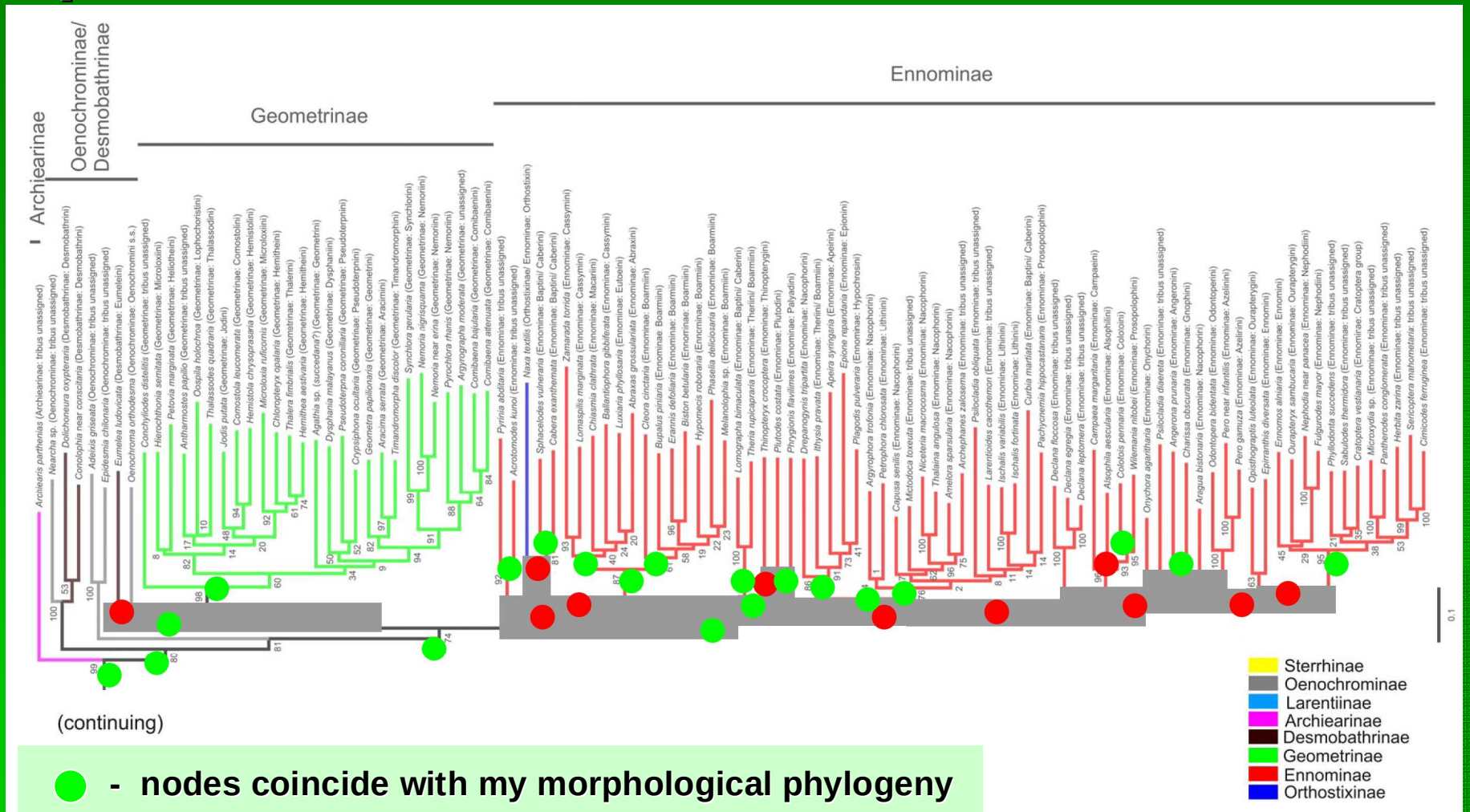
- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny

16. Sihvonen et al., 2011 – phylogenetic tree of Geometridae, first portion



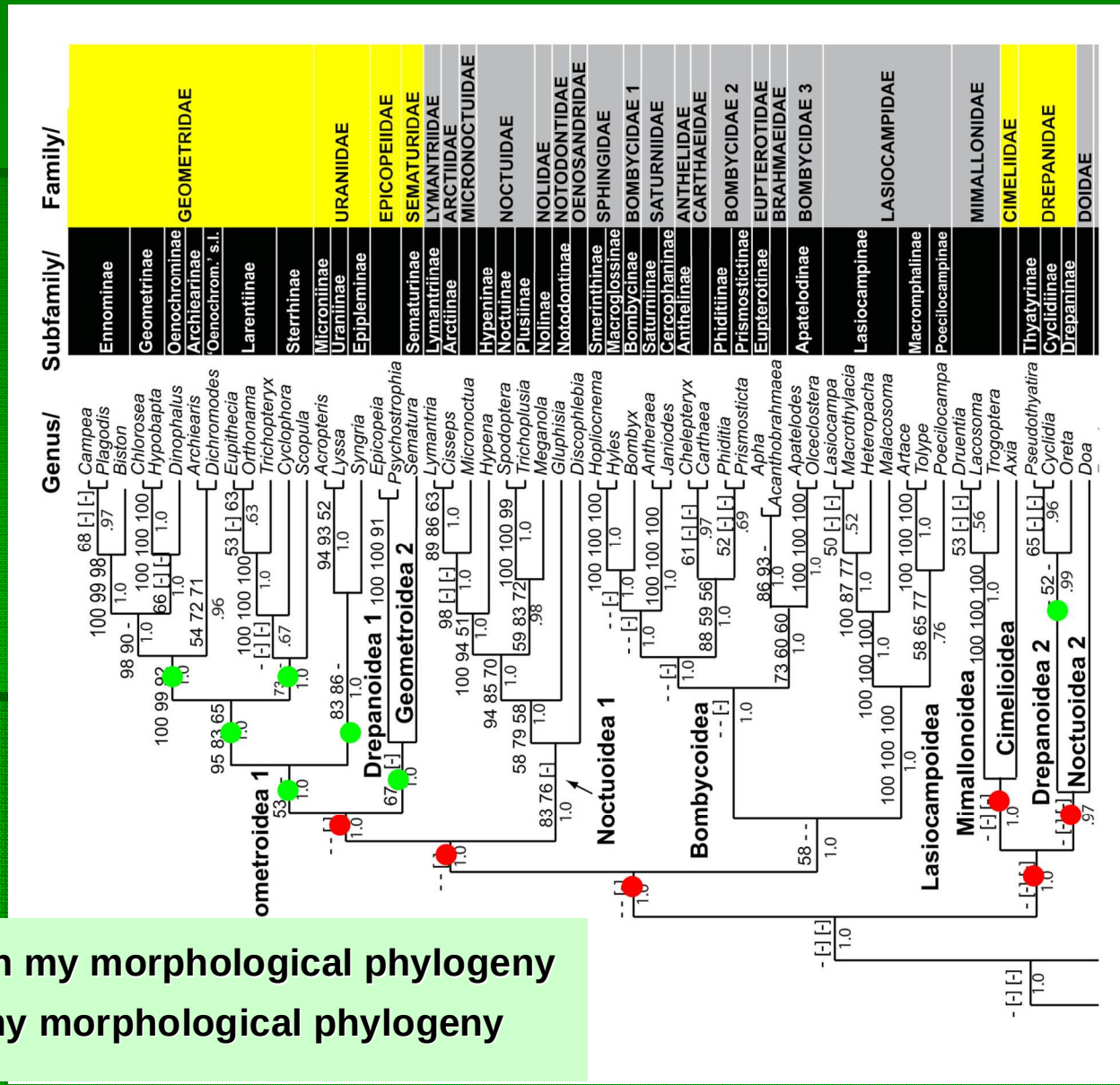
- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny
- "obscure area" – nodes with bootstrap value < 50

17. Sihvonen et al., 2011 – phylogenetic tree of Geometridae, second portion with the basal “obscure area” marked



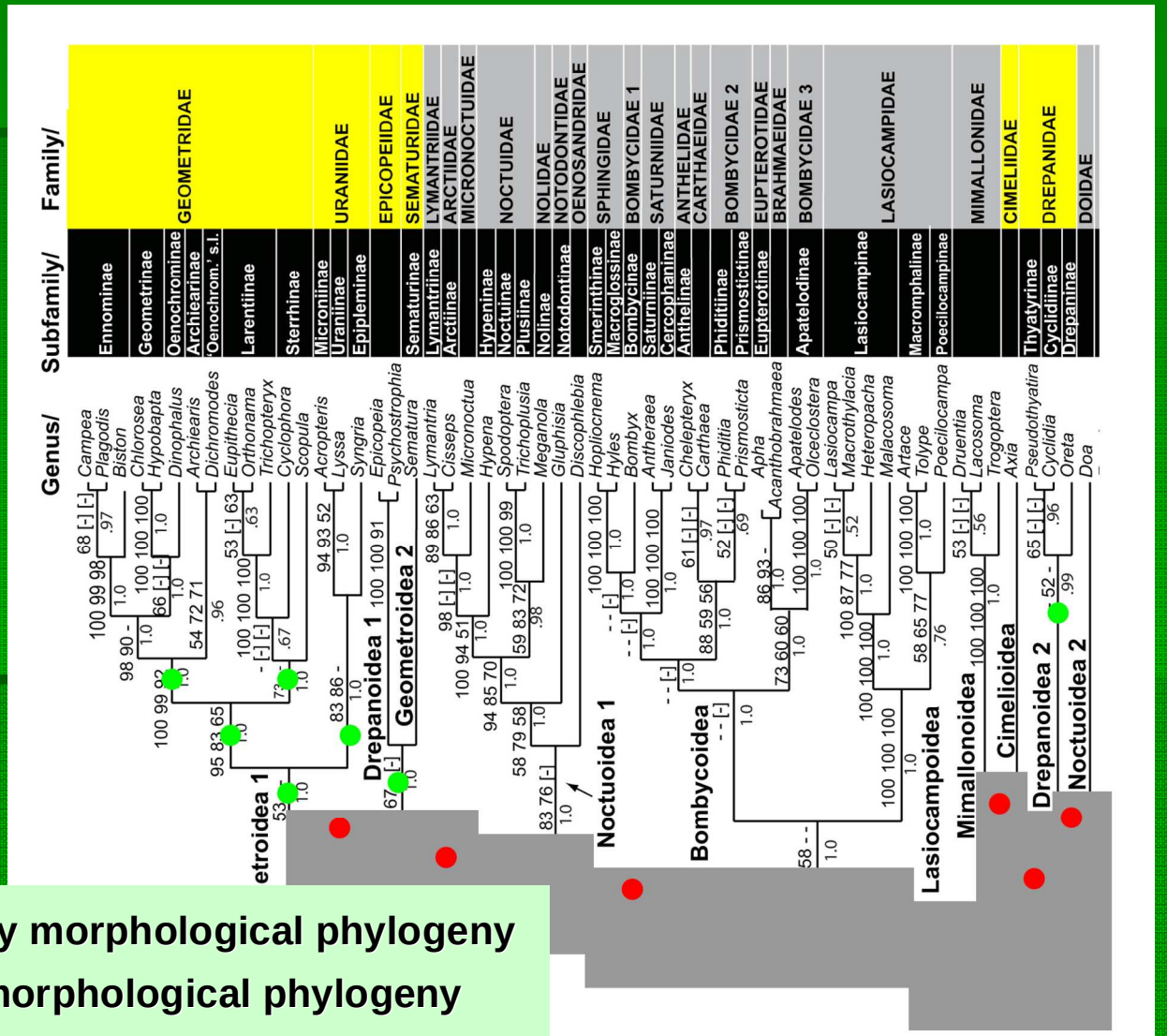
- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny
- “obscure area” – nodes with bootstrap value < 50

18. Regier et al., 2009 – phylogenetic tree of Lepidoptera, portion with geometroid families



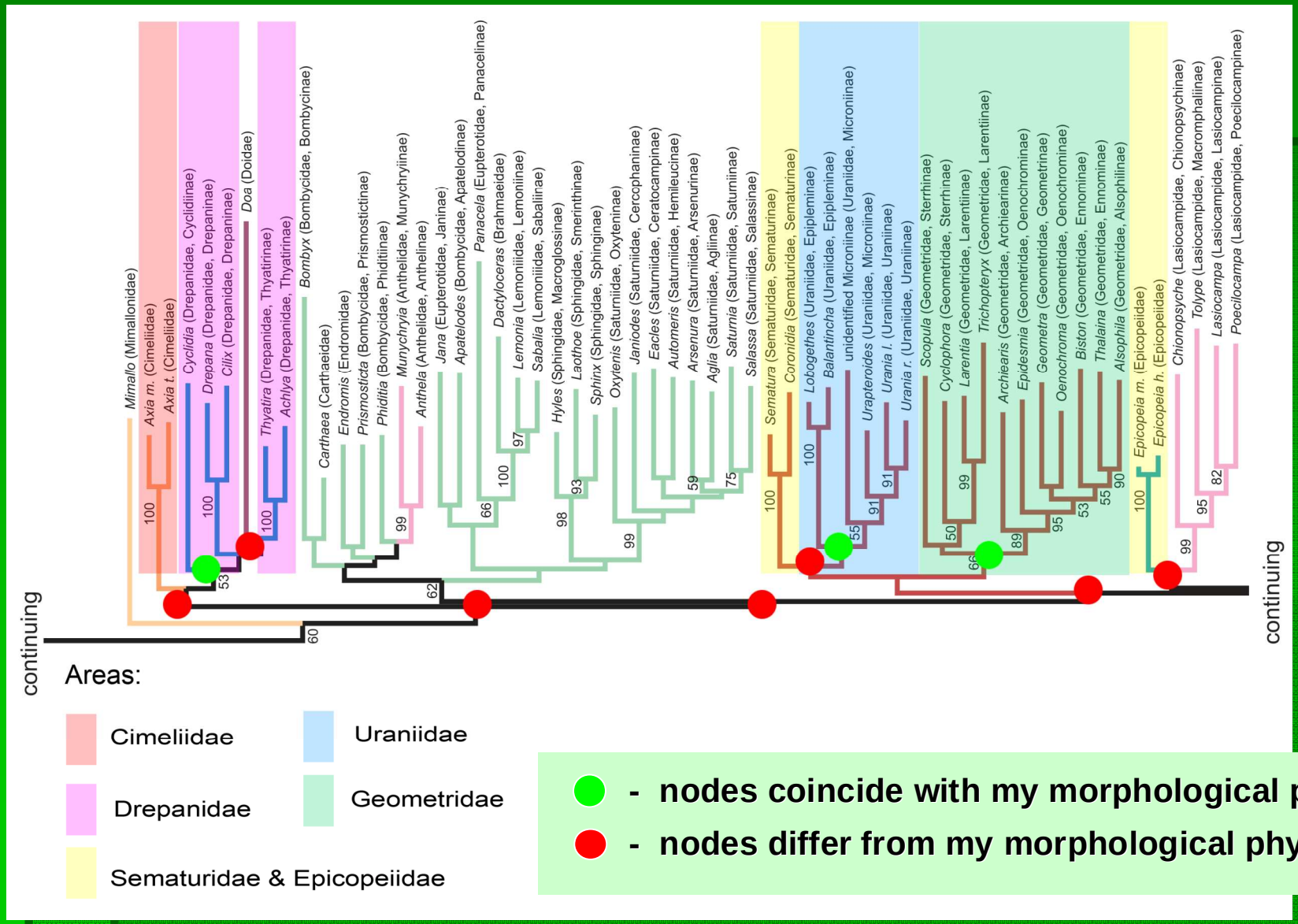
- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny

19. Regier et al., 2009 – phylogenetic tree of Lepidoptera, portion with geometroid families with the basal “obscure area” marked



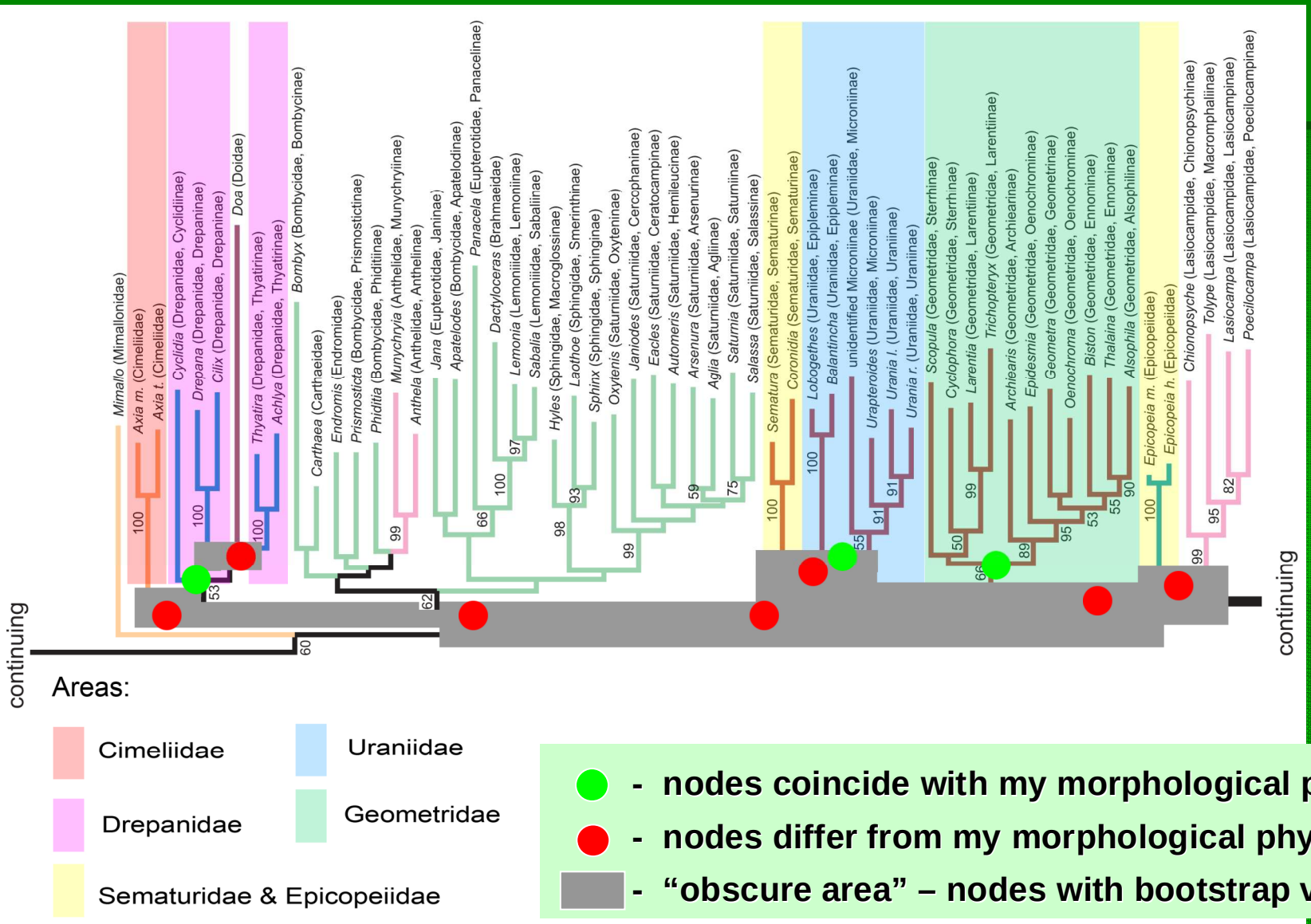
- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny
- “obscure area” – nodes with bootstrap value < 50

20. Mutanen et al., 2010 – phylogenetic tree of Lepidoptera, portion with geometroid families



- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny

21. Mutanen et al., 2010 – phylogenetic tree of Lepidoptera, portion with geometroid families with the basal “obscure area” marked



- nodes coincide with my morphological phylogeny
- nodes differ from my morphological phylogeny
- “obscure area” – nodes with bootstrap value < 50

Conclusion

- In the geometroid lepidopterans, modern morphological and molecular phylogenies demonstrate rather good concordance when the nodes of the latter have high value of BP support. The exceptions are rare and needs in special researches.
- Increasing of frequencies of sampling and growth of the length of analysed nucleotide sequence did not lead to growth of robustness of the resulting tress. In contrast, trees with less frequent sampling have higher value of BP support and more consistent with morphological data.
- Methods of the phylogenetic reconstructions in both approaches are fundamentally different: molecular data have to be analyzed by formal quantitative methods, whereas morphological ones are consistent with logic construction of the tree and immanently require the preliminary selection (a priori weighting) of characters based on the previous knowledge about the probability and probable directions of certain morphological transformations. Highest correspondence between the molecular and morphological phylogenies demonstrates just in this case.
- Supposedly, this concordance sourced from common theoretic basis of both approaches, which includes note on some degree of selective neutrality of the analysed characters and using of models of their evolution:

  - selective neutrality of most genomic mutation and models of DNA sequence evolution in the molecular phylogenetics;

  - probable selective neutrality of most used characters (85% from all 122 used characters, mainly from the genitalia and scent system (androconial apparatus) of males) and notions of general moduses (that is, models) of evolution of morphostructures in my morphological phylogeny.
- Taking into account the difference between the morphological and molecular characters, both types of data hardly by united for the "total evidence" phylogenetic approach. However, because of similar theoretic basis, they can be used for reciprocal testing of the results of phylogenetic reconstructions.

Thank you for your attention!