

ON THE PHYLOGENETIC RELATIONS IN THE BISTONINÆ (GEOMETRIDÆ), WITH SPECIAL REGARD TO *PÆCILOPSIS*

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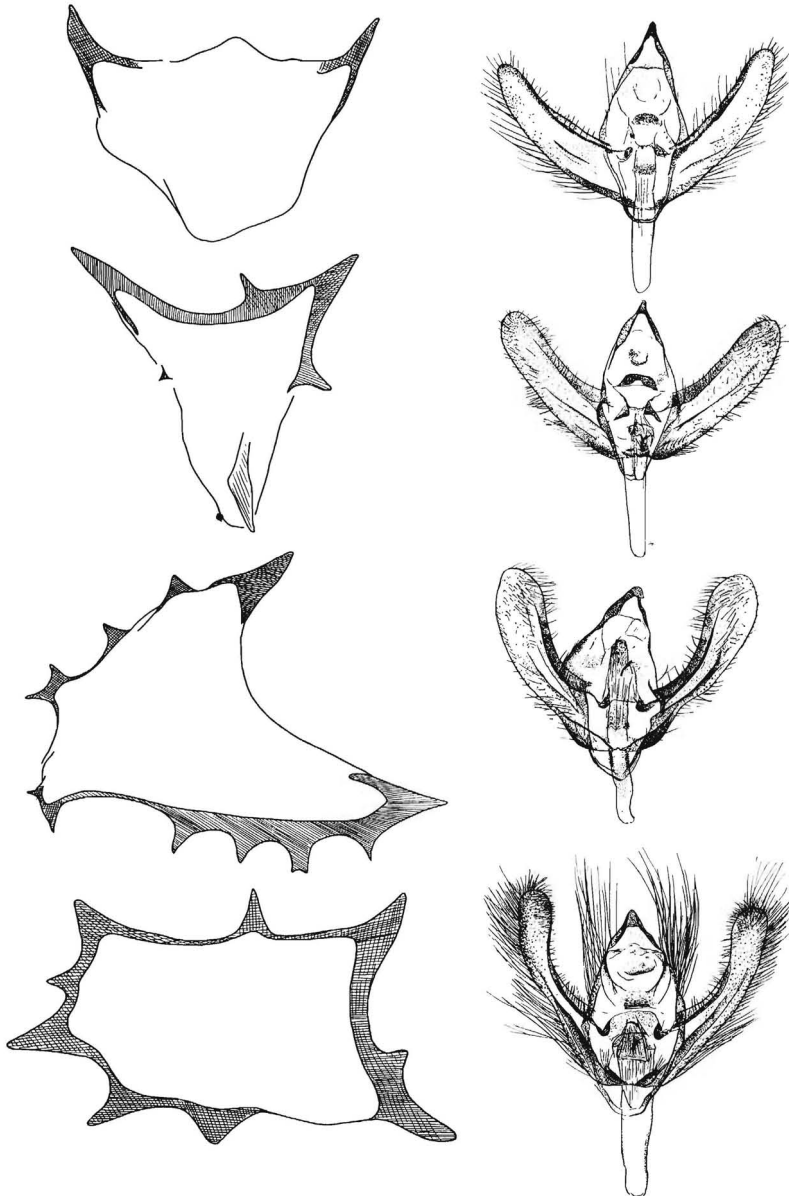
In our recent work (Povolný & Nosek, 1954) we tried to illustrate the position of *Pæciloipsis isabellæ* Harrison and its zoogeographic character. This was possible only in simultaneous comparison of several groups of the geometrid subfamily Bistoninæ, which resulted in some important viewpoints on the phylogenetical relations of this group. To illustrate them with special regard to the genus *Pæciloipsis* Harrison is the theme of this study. It is an agreeable duty to thank Dr. T. N. FREEMAN for providing us the single non-European species of *Pæciloipsis*—*P. rachelæ* Hulst—which we could not obtain in European institutions and for his very kind help in our work.

HARRISON was the first author pointing to the great heterogeneity of the old genus *Biston* Leach, towards the beginning of this century. In 1915 PROUT (in Seitz) gave a more progressive systematical conception of the Bistoninæ, if we compare it with that one of the older authors (STAUDINGER, SPULER, and others), though he does not include *P. isabellæ*. This conception by PROUT was based mostly upon external morphology (venation, legs and their spines, palpi, proboscis, etc.), and in limited dimension also upon anatomical criteria, though Pierce has in 1914 already published a good analysis of the genitalia of the British Bistoninæ. Pointing to the work mainly of HARRISON, PIERCE, and of other authors, similarly as to our own study, we do not intend to give once more a detailed morphological description of the single species, but we shall instead discuss the known facts from the viewpoint of phylogeny.

It is evident that the present Bistoninæ consist substantially of two large groups of genera and species. The first group contains older and mostly isolated species and genera. They all have a bifurcated ending of the uncus and mostly differentiated male genitalia. Two branches can be distinguished in this group. The first contains the forms related to *Biston strataria* Hfn. and *Amphidasis betularia* L., the second being certainly congeneric with the first. It seems very probable that these are simultaneously the forms connecting the Bistoninæ with the Ennominae (through *Gonodontis*), as indicated in 1913. This is shown in the presence of the wings in both sexes, and in the ecology, as *Biston* appear much later than other Bistoninæ, which appear mostly in the early spring. The other branch of the first group is represented by genera and species such as *Phigalia* (*pedaria* F.), *Macrobiston*, and *Apocheima* (*hispidaria* Schiff.). These belong to the true Bistoninæ and represent their older forms.

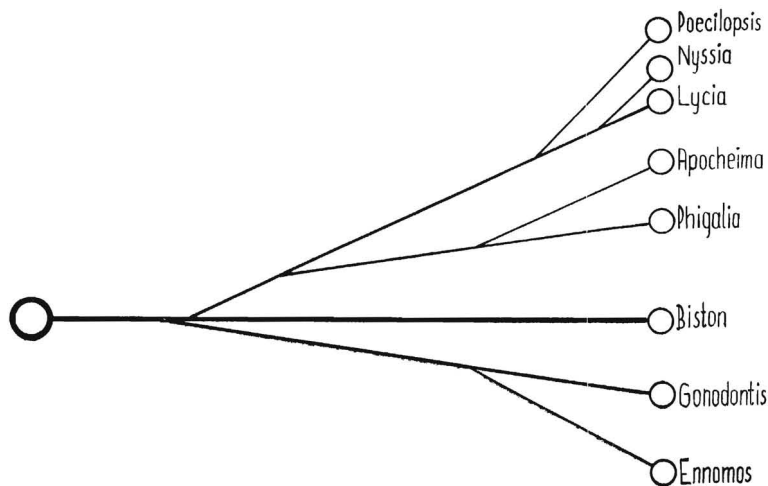
The second group is represented by the relatively very homogeneous forms of monophyletic origin, which must be also much younger than the first group. This is shown in their surprising morphological uniformity and simple genitalia. These forms are concentrated in three genera representing the single branches of development of this group. These genera are *Lycia* Hbn., *Nyssia* Dup. (*Ithysia* Hbn.) and *Pæciloipsis*, of which many forms are of strictly European origin. The close relation of this group is shown not only in morphology but also genetically, because most species tend to rich hybridization.

In contrast to the first group, whose members are distributed on the enormous Palearctic area and penetrate also northern America, the distribution of many members of the second group is more limited, and some are strictly European.



Top, *P. lapponaria*; second, *P. pomonaria*; third, *P. isabellæ*; bottom, *P. rachelæ*.  
(Female signum bursæ left; male genitalia right.)

Ecologically the two groups also differ greatly. Whereas members of the first group feed only on trees, those of the second are in their majority adapted to herbaceous plants. The first group are, indeed, forest-forms; in the second group inhabitants of prairies prevail. The oldest forms of the second group are contained in the genus *Lycia* (*hirtaria* and *ursaria*) representing the surviving branch of the primitive early Bistoninæ. The second two branches (*Nyssia* and *Pœcilopsis*) are the youngest genera of the Bistoninæ. HARRISON (1913) considered *Pœcilopsis* younger than *Nyssia*, but it is very difficult to decide exactly the relative age of these two groups. Much more, it seems that they are both young, independent parallel branches of the Bistoninæ.



The species of *Nyssia* are decided inhabitants of herbaceous growth and centered in central Europe, whereas *Lycia* and *Biston* (*s. str.*) are of Siberian origin. HARRISON (1913) considered *Nyssia zonaria* Schiff. the most specialized *Nyssia*. It is to point, however, that this species has a wider distribution than all other *Nyssia* and is rather polyphagous. The circumstances show that *N. zonaria* is an eurytopic species, whereas the other *Nyssia* are specialised stenotopic forms of the Alps and of the mountains of the Balkans. Some of them are *in statu nascendi*, representing plastic and recently originating forms.

*Pœcilopsis* contains four species (*pomonaria* Hbn., *isabellæ*, *lapponaria* Bois., and *rachelæ*), *P. pomonaria* being original and comparatively isolated. Morphologically the species are very close, but evidently *P. pomonaria* is closely related to *P. isabellæ*, whereas *P. lapponaria* and *P. rachelæ* are in development. In contrast to *Nyssia*, which are oligophagous, *Pœcilopsis* are substantially polyphagous forms inhabiting various trees of forests and plants in the boreal prairies. Though we can see the tendency to foodplant specialization in some of them, it is evident that they must have been polyphagous, as most of them they can be reared on *Betula*, *Cratægus*, *Salix*, etc. The broadest polyphagy is seen in *P. pomonaria*, feeding mostly various forest trees (*Quercus*, *Cratægus*,

but also *Malus*, etc.), whereas *P. isabellæ* is specialised on *Larix*. *P. lapponaria* feeds on various herbs (*Erica*, *Calluna*), but also trees (*Betula*, *Crataegus*), and about *P. rachelæ* HARRISON writes that this species "has a similar weakness for dwarf willows on the prairies". It seems that *P. pomonaria* is the derivate of the ancestral *Pæcilopsis*-form living in the Eurasiatic forest-zone of mild climate. The specialization of these forms in the European region on the deciduous conifer *Larix* produced *P. isabellæ*. The populations of the boreal forests developed to *P. lapponaria* in Europe and to *P. rachelæ* in northern America.

Some authors have presumed that *P. lapponaria* and *P. isabellæ* in Europe are of boreoalpine history and of postglacial origin. Respecting not the fact that *P. isabellæ* Harr. is related more with *P. pomonaria* Hbn. than with *P. lapponaria* Boisd., we see further convincing facts showing the contrary. BEIRNE (1947) proved that even much longer periods than Holocene (about 20,000 years) were not sufficient for developing species by the isolation of *P. lapponaria* and *Nyssia zonaria* in the British Isles, where the presence of *P. lapponaria* is from the first würm-stadial (120,000 years) and of *N. zonaria* from the first würm-interstadial age (80,000 years), building races differing little from the continental populations. *P. isabellæ* is closely dependent upon the European *Larix*, which has nothing to do with the European glacial-period, and their histories are in common. *P. isabellæ* was carried beyond the original area of the European *Larix* by the activity of the man, and in certain secondary habitats it may cause great damage on its foodplant. It is to be decided, finally, what route brought *P. rachelæ* to its present native country. The close relationship between *P. lapponaria* and *P. rachelæ*, and the present known distribution of *P. lapponaria* suggest the possible historical connection through the presumed continental bridge of Iceland and the present islands of the northern Atlantic. However, the eastern distribution of *P. lapponaria* and its limits in Europe or Asia, and the western distribution of *P. rachelæ* in Canada are not known.

It is to be concluded that Bistoninae are of Angarian origin. The differentiation of the first group (*Biston*, *Phigalia*, *Apocheima*) must have been finished in the upper Pliocene there. Towards its end the mighty stream of the Angarian fauna was drawn westwards by the climatic changes of the starting glacial and in the European region the specialization and development of the Bistoninae was continued in the Pleistocene by the origin of *Nyssia* and *Pæcilopsis*. The first of them developed by specialisation to the herbaceous vegetation in the Alps and Balkans. The second originated in the forests of central and northern Europe. The origin and distribution of *Pæcilopsis rachelæ* requires further study.

#### References

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