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One century after: a reappraisal of the gnathos (*sensu* Pierce, 1914) in Larentiinae (Lepidoptera: Geometridae)

OLGA SCHMIDT

Staatliche Naturwissenschaftliche Sammlungen Bayerns, Zoologische Staatssammlung München, Münchhausenstraße 21, 81247, Munich, Germany. E-mail: Olga.Schmidt@zsm.mwn.de

Abstract

One century ago, F.N. Pierce in his well-known monograph on the genitalia of Geometridae (Lepidoptera), divided the family into two major subdivisions, the Gnathoi and the Agnathoi, depending on the presence or absence of the gnathos in males. In his study, Pierce assigned the Larentiinae to the Agnathoi based on the apparent absence of the gnathos in this subfamily. A re-examination of the male genitalic characters of numerous larentiine species representing 14 different tribes provided, contrary to Pierce's results, evidence for the presence of the gnathos in Larentiinae. Illustrations of the gnathos (or its remnants) in male genitalia of selected species are provided and the value of the uncus and gnathos for inferring phylogenetic relationships is discussed.

Key words: anal tube, Asthenini, Cataclymini, Chesiadini, Cidariini, Euphyiini, geometrid moths, gnathos, higher-rank classification, homology, Hydriomenini, larentiine moths, male genitalia, morphology, Operophterini, Phileremini, Stammadini, Trichopterygini, Triphosini, Xanthorhoini

Introduction

A century ago F.N. Pierce (1914) published his monograph "The Genitalia of the Group Geometridae of the Lepidoptera of the British Islands". F.N. Pierce was a pioneer in using moth genital characters for taxonomic purposes and acquired a broad knowledge of these structures. He divided the family Geometridae into two major divisions and termed them Gnathoi and Agnathoi, depending on the presence or absence of the gnathos in male genitalia, and assigned the Larentiinae to the Agnathoi. For many decades his classification was generally accepted (see Prout 1939, Craw 1986, Holloway 1997, Rajaei *et al.* 2011, Viidalepp 2011, Hausmann & Viidalepp 2012, Li *et al.* 2012). Recent studies of the male genital musculature in the subfamily Larentiinae (see Schmidt 2001, 2013, 2014a) provided some new insights about the configuration, articulation and fusion of sclerites, and led to doubts regarding the absence of the gnathos in larentiines.

As stated by Pierce (1914) and Klots (1970), the gnathos is a band-like process attached to the caudal margin of the tegumen on each side, ventrad of the uncus, enclosing the anal tube. The shape of the gnathos and the way it is connected to the uncus and to the tegumen exhibit a high level of variation. In most of non-larentiine geometrids the gnathos arms are well pronounced and fused medially. However, in some of the genera the gnathos is rather weakly developed (*e.g.* *Alsophila* Hübner, *Hypobapta* Prout), consisting of two distinctly separate arms (*e.g.* *Cheimoptena* Danilevsky, *Leucobrephos* Grote, *Ozola* Walker), or conspicuously modified so that in *Crypsiphona* Meyrick and *Paraterpna* Goldfinch the gnathos arms are fused with the membrane of the diaphragma medially dorsad of the aedeagus (see Pitkin *et al.* 2007).

Until recently, the presence of the gnathos in the male genitalia of larentiine moths was considered as a peculiar character shared by several genera assigned to the tribe Trichopterygini (*e.g.* *Chrioloba* Prout, *Goniopteroloba* Hampson, *Ptygmatophora* Gumpfenberg, *Syzeuxis* Hampson, *Tyloptera* Christoph). In the larentiines, apart from Trichopterygini, the presence of the gnathos arms was only noted in *Aponotoreas* Craw, *Laciniodes* Warren, *Pseudostegania* Butler and *Solitanea* Djakonov (see Craw 1986, Beljaev 2008, Han *et al.* 2010). Images of male genitalia of larentiines sometimes show the areas of sclerotization of the tegumen ventrad of