



<http://dx.doi.org/10.11646/zootaxa.3856.3.6>

<http://zoobank.org/urn:lsid:zoobank.org:pub:22A34292-15B9-4FF3-A7E0-BF68323D89E2>

Comparison of the structure and musculature of male terminalia in the tribe Cidariini Duponchel (Lepidoptera: Geometridae: Larentiinae) once again throws into doubt a sister relationship with the Xanthorhoini

OLGA SCHMIDT

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

Abstract

The structure and musculature of the male terminalia are described and illustrated in 11 genera of the tribe Cidariini (Lepidoptera, Geometridae, Larentiinae) from the Holarctic and Oriental regions. Nine genital muscles were identified: m1, m2(10), m3(2), m4, m5(7), m6(5), m7(6), m8(3) and m21. Variation in the insertion of the muscles m1, m3(2), m4, m5(7), m6(5) and m8(3) on the sclerites in several generic groups of the tribe Cidariini is discussed, revealing that the *Thera* species group does not share some apparently cidariine characters. A comparative analysis of the musculature in the tribes Cidariini and Xanthorhoini questions the sister relationship of these tribes that was suggested by earlier studies. The application of the terms ‘anellus lobes’ and ‘labides’ is discussed.

Key words: anellus lobes, cidariine moths, Eupitheciini, geometrid moths, higher-rank classification, Holarctic region, homology, labides, larentiine moths, male genitalia, morphology, muscles, Oriental region, Xanthorhoini

Introduction

The structure and musculature of male terminalia proved to be beneficial for the higher-rank classification of Lepidoptera (see Kuznetsov & Stekolnikov 1986, 2001). However, the knowledge of morphology and function of the male genitalic musculature in the subfamily Larentiinae (Lepidoptera, Geometridae) remains limited. In this regard, a group of tribes formerly treated as Xanthorhoini *s. l.* and characterized by the presence of coremata associated with the eighth abdominal segment in males has been reviewed recently by Schmidt (2013). The male genital musculature of only a few cidariine species have been examined so far, whereby a thorough review was beyond the scope of previous studies (*e.g.* Razowskj & Wojtusiak 1981, Kuznetsov & Stekolnikov 2001, Valersky 2011).

The larentiine moth tribe Cidariini is distinguished by a combination of characters (see Choi 1997a, Hausmann and Viidalepp 2012), including the extended anellus lobes (labides) connected to the juxta. The tribe has a long history of discussion since the introduction of the name by Duponchel (1845). Different aspects of the tribe Cidariini have been reviewed by Pierce (1914), Patočka (1995), Patočka and Turčáni (2005), Holloway (1997), Choi (1997a–b, 1998a–c, 2000a–c, 2001, 2002b, 2003, 2006), Viidalepp and Kostjuk (2005), Viidalepp (1996, 2003, 2011), Hausmann and Viidalepp (2012). Selected species-groups and genera were examined by Prout (1940), Forbes (1948), McGuffin (1958), Herbulot (1962), Heitzman and Enns (1978), Inoue (1982), Hodges (1983), Viidalepp (1980, 1988), Rezbanyai-Reser (1990), Xue and Zhu (1999), Ebert (2001), Beljaev & Vasilenko (2002), Hausmann & Parra (2009), Karsholt *et al.* (2013). The taxonomic data on the genera and species were compiled by Scoble (1999). During the past decade, a few species of the tribe Cidariini have been included in molecular analyses, providing phylogenies of the family Geometridae (Abraham *et al.* 2001, Snäll *et al.* 2007, Yamamoto & Sota 2007, Strutzenberger *et al.* 2010, Hausmann *et al.* 2011, Sihvonen *et al.* 2011).

The following four distinguishable groups of genera in the European Cidariini were identified and unifying characters presented by Hausmann and Viidalepp (2012): (1) *Thera* Stephens, 1831 and related genera (*Pennithera* Viidalepp, 1980, *Heterothera* Inoue, 1943); (2) *Colostygia* Hübner, 1825, *Electrophaes* Prout, 1923, *Chlorochlysta*

of membrane which closes the posterior end of the abdomen, extending from the tegumen and the anal tube dorsally to the base of the valvae and the vinculum ventrally (Klotz 1970). The aedeagal anellus was described by Pierce (1914) as a projection into which the aedeagus is withdrawn. According to Pierce (1914), “the anellus may also be extended into two lateral lobes which are termed anellus lobes”. He also introduced the term ‘labides’ as follows, “Springing from the points of union of the transtilla with the costae, there may arise two long arms, each bearing a soft hairy pad, and united together by a thin membrane”, as in the genus *Eupithecia* Curtis. However these terms are ambiguous. The eupitheciine labides are not always united together medially and the anellus lobes *sensu* Pierce are sometimes long and connected to the base of the costa valvae and often to the transtilla by a membranous band. These overlapping similarities confuse this terminology. Kristensen (2003) pointed out that the anellus lobes, “probably pertain morphologically to a basal valve territory”, which is apparently characteristic of the labides as well. Moreover, Holloway (1997) noted that the cidariine anellus lobes have an “almost filamentous ventral extension towards the juxta suggestive of homology with the eupitheciine labides”. The matter is even more complicated as only the dorsal arms arising from the base of the costa valvae were termed ‘the labides’ by Pierce (1914). Some authors (*e.g.* Holloway 1997, Choi 2002a) were using this term *sensu* Pierce. However, most of subsequent authors publishing on the larentiine moths (*e.g.* Mironov 2003, Beljaev 2008, Viidalepp 2011, Hausmann & Viidalepp 2012) were using this term in a broadened sense, defining the posterior projections (=arms) of the labides, which are congruent to the ‘labides’ *sensu* Pierce and, additionally, the anterior projections usually connected to the juxta. A broad application of this term is supported in this paper as the anterior projections directed towards the juxta are connected to the labides *sensu* Pierce and seem to be part of a compound structure.

Beljaev (2006, 2008) considered that most of the anellar structures located between the juxta and the valvae in the Geometroidea are homologous. A review of the annular structures in the Geometroidea is beyond the scope of the present paper, however, the structure and modifications of the labides in the Larentiinae will be discussed in a subsequent publication (Schmidt, in prep.).

A thorough phylogenetic analysis of this group with appropriate and sufficient taxon sampling, well chosen morphological characters and selection of relevant outgroup taxa is required for obtaining an accurate phylogenetic reconstruction and for evaluating the homologies of the genital sclerites.

Acknowledgements

The research was conducted over more than twenty years in several institutions, including the Saint Petersburg State University (Russia), the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia), the Zoological Institute and Zoological Museum of the University of Hamburg (Germany), State Museum of Natural History (Stuttgart, Germany) and the Zoologische Staatssammlung (Munich, Germany). Grateful thanks to Catherine Byrne (Tasmanian Museum and Art Gallery, Hobart) for her vivid interest in the subject and thorough review of my manuscript. Sincere thanks to Evgeny Beljaev (Institute of Biology and Soil Science of the Far Eastern Branch of Russian Academy of Sciences, Vladivostok, Russia) for sharing his well-grounded point of view on the terminology and sclerite homology of the genitalia within the family Geometridae and their allies and for helpful comments on the manuscript. Many thanks to Axel Hausmann (ZSM) for collecting several cidariine specimens for me and providing valuable comments on the manuscript. Stefan Schmidt (ZSM) is acknowledged for support.

References

- Abraham, D., Ryrholm, N., Wittzell, H., Holloway, J.D., Scoble, M.J. & Löfstedt, C. (2001) Molecular phylogeny of the subfamilies in Geometridae (Geometroidea: Lepidoptera). *Molecular Phylogenetics and Evolution*, 20, 65–77.
<http://dx.doi.org/10.1006/mpev.2001.0949>
- Beljaev, E.A. (2006) A morphological approach to the Ennominae phylogeny (Lepidoptera, Geometridae). *Spixiana*, 29 (3), 215–216.
- Beljaev, E.A. (2008) Phylogenetic relationships of the family Geometridae and its subfamilies (Lepidoptera). *Meetings in memory of N.A. Cholodkovsky*, 60, 1–238. [in Russian]
- Beljaev, E.A. & Vasilenko, S.V. (2002) An annotated checklist of geometrid moths (Lepidoptera: Geometridae) from the Kamchatka Peninsula and adjacent islands. *Entomologica Fennica*, 13, 195–235.
- Choi, S.-W. (1997a) A phylogenetic study on genera of the Cidariini from the Holarctic and the Indo-Australian areas

- (Lepidoptera: Geometridae: Larentiinae). *Systematic Entomology*, 22, 287–312.
<http://dx.doi.org/10.1046/j.1365-3113.1997.d01-49.x>
- Choi, S.-W. (1997b) *Systematics of the Cidariini (Lepidoptera: Geometridae, Larentiinae)*. Helsinki, 178 pp.
- Choi, S.-W. (1998a) Systematics of the genus *Heterothena* Inoue (Lepidoptera, Geometridae: Larentiinae). *Tijdschrift voor Entomologie*, 141, 19–47.
<http://dx.doi.org/10.1163/22119434-99900003>
- Choi, S.-W. (1998b) Systematics of the genus *Cidaria* Treitschke (Lepidoptera, Geometridae, Larentiinae). *Zoological Journal of the Linnean Society*, 122, 555–580.
<http://dx.doi.org/10.1111/j.1096-3642.1998.tb02163.x>
- Choi, S.-W. (1998c) Taxonomy of the genus *Plemyria* Hübner (Lepidoptera, Geometridae, Larentiinae). *Entomologica Fennica*, 9, 185–196.
- Choi, S.-W. (2000a) Cladistic biogeography of the moth tribe Cidariini (Lepidoptera, Geometridae) in the Holarctic and Indo-Chinese regions. *Biological Journal of the Linnean Society*, 71, 529–547.
<http://dx.doi.org/10.1111/j.1095-8312.2000.tb01273.x>
- Choi, S.-W. (2000b) The occurrence of *Lampropteryx suffumata* (Denis & Schiffermüller) (Lepidoptera, Geometridae) in North America. *Pan-Pacific Entomologist*, 70 (2), 123–125.
- Choi, S.-W. (2000c) A cladistic analysis of the Therini: A new synonym of the Cidariini (Lepidoptera: Geometridae, Larentiinae). *American Museum Novitates*, 3295, 25 pp.
- Choi, S.-W. (2001) Phylogeny of *Eulithis* and related genera (Lepidoptera, Geometridae), with an implication of wing pattern evolution. *American Museum Novitates*, 3318, 1–37.
[http://dx.doi.org/10.1206/0003-0082\(2001\)318<0001:POEHBA>2.0.CO;2](http://dx.doi.org/10.1206/0003-0082(2001)318<0001:POEHBA>2.0.CO;2)
- Choi, S.-W. (2002a) Two New Larentiinae Species (Lepidoptera: Geometridae) from Korea. *Korean Journal of Entomology*, 32 (1), 57–60.
- Choi, S.-W. (2002b) Taxonomy of the Cidariini (Lepidoptera: Geometridae) in Korea (1). *Korean Journal of Entomology*, 32 (4), 205–222.
- Choi, S.-W. (2003) Faunistic study of the Larentiinae (Lepidoptera: Geometridae) of North Korea (1). *Insecta Koreana*, 20 (3–4), 313–342.
- Choi, S.-W. (2006) Cladistic analysis of the tribe Xanthorhoini in the Holarctic region (Lepidoptera, Geometridae). *Spixiana*, 29 (3), 201–202.
- Curtis, J. (1834) *British Entomology: the genera of insects. Vol. 2*. Printed for the author, London, 518 pp.
- Duponchel, M.P.A.J. (1845) *Catalogue méthodique des lépidoptères d'Europe distribués en familles, tribes et genres*. Méquignon-Marvis fils., Paris, 583 pp.
- Ebert, G. (2001) *Die Schmetterlinge Baden-Württembergs, Band 8—Nachtfliegen VI*. Stuttgart (Hohenheim), Ulmer, 541 pp.
- Ferguson, D.C. (1983) Larentiinae. In: Hodges, R.W., Dominick, T., Davis, D.R., Ferguson, D.C., Flanclemont, J.G., Munroe E.G. & Powell, J.A. (Eds.), *Check List of the Lepidoptera of America North of Mexico*. E.W. Classey limited and the Wedge Entomological Research Foundation, London, pp. 101–107.
- Forbes, W.T.M. (1948) Lepidoptera of New York and neighbouring states, part 2. *Cornell University Agricultural Experimental Station Memoir*, 274, 128–175.
- Hausmann, A., Haszprunar, G. & Hebert, P.D.N. (2011) DNA barcoding the Geometrid fauna of Bavaria (Lepidoptera): successes, surprises, and questions. *PLoS ONE*, 6, e17134.
<http://dx.doi.org/10.1371/journal.pone.0017134>
- Hausmann, A. & Parra, L.E. (2009) An unexpected hotspot of moth biodiversity in Chilean northern Patagonia (Lepidoptera, Geometridae). *Zootaxa*, 1989, 23–38.
- Hausmann, A. & Viidalepp, J. (2012) Larentiinae I. In: Hausmann, A. (Ed.), *The Geometrid Moths of Europe 3*. Apollo Books, Stenstrup, pp. 1–743, 25 pl., 147 text-figs, 268 maps.
<http://dx.doi.org/10.1111/j.1748-5967.2002.tb00010.x>
- Heitzman, R.L. & Enns, W.R. (1978) Annotated list and keys to the geometrid subfamily Larentiinae (Lepidoptera: Geometridae) of Missouri. *Transactions of the Missouri Academy of Sciences*, 12, 47–63.
- Herbulot, C. (1962) Mise a jour de la liste des Geometridae des France. *Alexanor*, 2 (4), 117–124.
- Holloway, J.D. (1997) The Moths of Borneo: family Geometridae, subfamilies Sterrhinae and Larentiinae. *Malayan Nature Journal*, 51, 1–242.
- Inoue, H. (1982) *Moths of Japan. Vol. 1–2*. Kodansha, Tokyo, 966 pp. & 552 pp.
- Karsholt, O., Nieuwerkerken, E.J. van & de Jong, Y.S.D.M. (2013) Lepidoptera, Moths. Fauna Europaea. Version 2.6.2. Available from: <http://www.faunaeur.org> (accessed 29 August 2013)
- Klots, A.B. (1970) Lepidoptera. In: Tuxen, S.L. (Ed.), *Taxonomist's Glossary of Genitalia in Insects*. Munksgaard, Copenhagen, pp. 115–130.
- Kristensen, N.P. (2003) Skeleton and muscles: adults. In: Kristensen, N.P. (Ed.), *Lepidoptera, Moths and Butterflies. Morphology, Physiology and Development, vol. 2. Handbook of Zoology. Vol. 4. Part 36. Lepidoptera, Moths and Butterflies. Morphology, Physiology and Development. Vol. 2*. Walter de Gruyter, Berlin, pp. 39–131.
- Kuznetsov, V.I. & Stekolnikov, A.A. (1986) Classification of the higher taxa of Lepidoptera taking into account the results on comparative morphology of genitalia. *Trudy Vsesoyuznogo Entomologicheskogo Obshchestva*, 68, 42–46. [in Russian]
- Kuznetsov, V.I. & Stekolnikov, A.A. (2001) New approaches to the system of Lepidoptera of the world fauna (on the base of functional morphology of abdomen). *Proceedings of the Zoological Institute of St. Petersburg*, 282, 1–462. [in Russian]

- McGuffin, W.C. (1958) Larvae of the Nearctic Larentiinae. *Canadian Entomologist*, Supplement 8, 5–104.
- Mironov, V. (2003) Larentiinae II (Perizomini and Eupitheciini). In: Hausmann, A. (Ed.), *The geometrid moths of Europe 4*. Apollo Books, Stenstrup, pp. 1–463.
- Nichols, S.W. (Ed.) (1989) *The Torre-Bueno Glossary of Entomology*. New York Entomological Society in corporation with American Museum of Natural History, New York, 840 pp.
- Patočka, J. (1995) Die Puppen der Spanner Mitteleuropas, Unterfamilie Larentiinae, Tribus Lythriini, Xanthorhoini, Larentiini und Cidariini (Lepidoptera, Geometridae). *Deutsche Entomologische Zeitschrift*, 42, 139–174.
<http://dx.doi.org/10.1002/mmnd.19950420113>
- Patočka, J. & Turčáni, M. (2005) *Lepidoptera Pupae. Central European Species*. Apollo Books, Stenstrup, 542 pp.
- Pierce, F.N. (1914) *The Genitalia of the Group Geometridae of the Lepidoptera of the British Islands*. F.N. Pierce, The Elms, Dingle, Liverpool, 230 pp.
- Prout, L.B. (1912) Lepidoptera Heterocera, Fam. Geometridae, subfam. Hemitheinae. In: Wytsman, P. (Ed.), *Genera insectorum*, 129. Verteneuil & L. Desmet, Bruxelles, pp. 1–274.
- Prout, L.B. (1940) Larentiinae. In: Seitz, A. (Ed.). *Die Gross-Schmetterlinge der Erde*. Fauna Indo-Australica, Bd. 12, Alfred Kernen Verlag, Stuttgart, pp. 1–356.
- Razowskj, J. & Wojtusiak, J. (1981) Musculature of the male genitalia in Geometridae (Lepidoptera). *Folia Biologica*, 29 (3–4), 259–274.
- Rezbanyai-Reser, L. (1990) *Nebula achromaria* Lah. und *Psodos alpinata* Scop.: Berichtigung zu den Genitalabbildungen in Bleszynski 1965–1966 und Forster & Wohlfahrt 1980 (1981) (Lepidoptera, Geometridae). *Entomologische Zeitschrift mit Insektenbörse*, 100 (7), 126–131.
- Snäll, N., Tammaru, T., Wahlberg, N., Viidalepp, J., Ruohomäki, K., Savontaus, M.-L. & Huoponen, K. (2007) Phylogenetic relationships of the tribe Operophterini (Lepidoptera, Geometridae): a case study of the evolution of female flightlessness. *Biological Journal of the Linnean Society*, 92, 241–252.
<http://dx.doi.org/10.1111/j.1095-8312.2007.00834.x>
- Schmidt, O. (2001) The Australian species of *Anachloris* Meyrick (Lepidoptera: Geometridae: Larentiinae): taxonomy, male genitalia musculature and systematic position. *Australian Journal of Entomology*, 40, 219–230.
<http://dx.doi.org/10.1046/j.1440-6055.2001.00232.x>
- Schmidt, O. (2013) The structure and musculature of male terminalia in the tribe Xanthorhoini Pierce and related tribes (Lepidoptera: Geometridae: Larentiinae), with particular reference to the Palearctic and Australian regions. *Zootaxa*, 3721 (6), 552–572.
<http://dx.doi.org/10.11646/zootaxa.3721.6.3>
- Scoble, M.J. (1995) *The Lepidoptera: Form, Function and Diversity*. Oxford University Press, Oxford, 424 pp.
- Scoble, M.J. (1999) *Geometrid Moths of the World: A Catalogue (Lepidoptera, Geometridae)*. CSIRO Publishing, Collingwood, Victoria, 1200 pp.
- Sihvonen, P., Mutanen, M., Kaila, L., Brehm, G., Hausmann, A. & Staude, H.S. (2011) Comprehensive Molecular Sampling Yields a Robust Phylogeny for Geometrid Moths (Lepidoptera: Geometridae). *PLoS ONE*, 6 (6), e20356.
<http://dx.doi.org/10.1371/journal.pone.0020356>
- Stephens, J.F. (1829–1831) *Illustrations of British Entomology. Haustellata*, 3. Baldwin and Cradock, London, 333 pp.
- Strutzenberger, P., Brehm, G., Bodner, F. & Fiedler, K. (2010) Molecular phylogeny of *Eois* (Lepidoptera, Geometridae): evolution of wing patterns and host plant use in a species-rich group of Neotropical moths. *Zoologica Scripta*, 39 (6), 603–620.
<http://dx.doi.org/10.1111/j.1463-6409.2010.00440.x>
- Tautel, C. & Billi, F. (2009) Description d'un nouveau taxon européen du genre *Thera*: *Thera firmata tyrrhenica* Tautel & Billi, 2009, n. ssp. (Lep. Geometridae Larentiinae). *Oreina*, 6, 20–24.
- Valersky, O.V. (2011) Musculature of the male terminalia in the geometrid moth subfamily Larentiinae (Lepidoptera, Geometridae). *Entomologicheskoe Obozrenie*, 90 (1), 82–104. [in Russian]
- Viidalepp, J. (1977) A list of Geometridae of the U.S.S.R. 2. *Entomologicheskoe Obozrenie*, 56 (3), 564–576. [in Russian]
- Viidalepp, J. (1980) Geometrid moths of the genus *Thera* Stph. in the fauna of the U.S.S.R. (Lepidoptera). *Tartu Riikliku Ülikooli Toimetised 516. Zooloogia-alaseid töid*, 13, 54–84. [in Russian]
- Viidalepp, J. (1988) *The Geometrid Moths of Mountainous Middle Asia*. Nauka, Moscow, 240 pp. [in Russian]
- Viidalepp, J. (1996) *Checklist of the Geometridae (Lepidoptera) of the former U.S.S.R.* Apollo Books, Stenstrup, 111 pp.
- Viidalepp, J. (2003) *Three different problems with "Thera" firmata (Hübner [1822])*. XXVI Nordic-Baltic Congress of Entomology, Skalupes, Latvia, July 6th to 13th, 2003. Programme, abstracts and list of participants, 30–40 pp.
- Viidalepp, J. (2011) A morphological review of tribes in Larentiinae (Lepidoptera: Geometridae). *Zootaxa*, 3136, 1–44.
- Viidalepp, J. & Kostjuk, I. (2005) *Pljushtshia prima*, new moth genus and species from Tadzhikistan (Lepidoptera, Geometridae). *European Journal of Entomology*, 103, 77–85.
- Xue, D.Y. & Zhu, H.F. (1999) *Fauna Sinica (Insecta: Lepidoptera: Geometridae: Larentiinae)*. Science Press, Beijing, China, 1099 pp. + 25 pls.
- 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.
<http://dx.doi.org/10.1016/j.ympev.2006.12.027>
- Young, C.J. (2006) Descriptions of the eggs of some southern Australian Geometridae (Lepidoptera). *Zootaxa*, 1287, 1–294, 143 plates.