A morphological approach to the Ennominae phylogeny (Lepidoptera, Geometridae)

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The Ennominae is the largest and, morphologically, most diversified subfamily in the Geometridae and the tribal composition and phylogeny of the subfamily are still far from being resolved. However modern molecular-phylogenetic investigations of the subfamily promise substantial breakthroughs in the construction of a meaningful phylogeny of the Ennominae (as well as of the Geometridae and other organisms). Nevertheless, in spite of the present predominant position of molecular-phylogenetic research in modern systematics, morphological analysis of organisms continues to be indispensable for the comprehension of taxonomy and evolution. Also, morphological analysis is irreplaceable for the definition of monophyletic groups, and even for the representational selection of specimens (samples) for molecular-phylogenetic analysis. A modern morphological tribal system and phylogeny for the Ennominae were proposed independently by Holloway (1994, 1997) and by Beljaev (1994). Here I propose a new hypothesis on basal branching in the Geometridae and Ennominae and tribal composition of the subfamily arising from the cladogram illustrated in Fig. 1.

In this analysis I applied direct weighting of characters based on comparative and functional-morphological analyses using outgroup comparison for the polarization of morphoclines. Structures of the anellar area of the male genitalia are mainly utilised in this investigation because they demon-

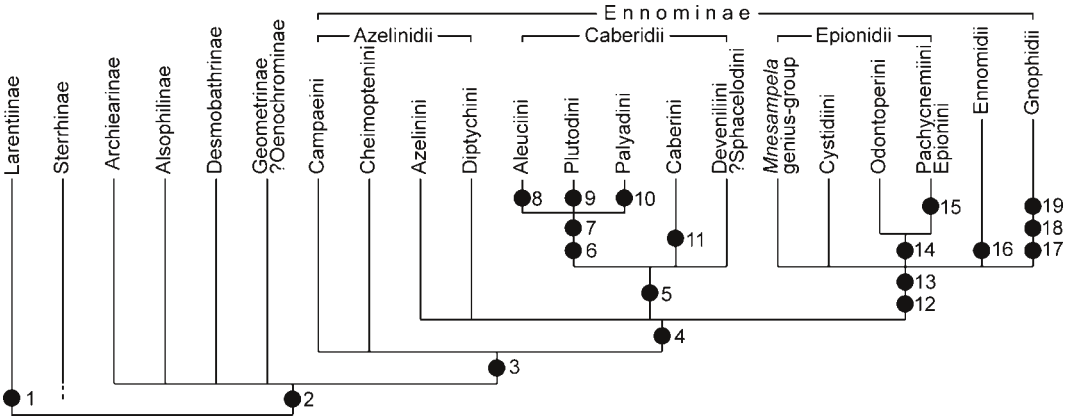

Fig. 1. Phylogenetic cladogram of basally derived branches in the Geometridae and Ennominae based on selected apomorpies. Apomorphies: **1,** labides which trend to medial shifting dorsad of aedeagus; **2,** labides removed from the bases of the valvae ventro-medially and which have approximately sagittal orientation of their bases; **3,** vein M_2 on hindwing lacking; **4,** signum deeply invaginated, toothed, sclerotized, hollow (mushroom-like); **5,** labides with bases orientated in frontal plane; **6,** cristae strongly developed; **7,** juxta broad, laterally almost reach base of transtilla; **8,** cristae integrated into juxta; **9,** sacculi with pointed and curved distal process; **10,** socii enlarged; **11,** sacculi articulated to each other directly, often connected to each other with traverse sclerotized bar; juxta placed posterior of sacculi; **12,** transtilla shaped as flat sclerite smoothly proceeds into costa of valva and possessing ventral process; **13,** muscle m_4 attached to transtilla mediad of *m2*, *m2* and *m4* crossed; **14,** labides flattening, horn-like, intromitted into ductus bursae at the copulation; **15,** labides with dorsal end of basis far from base of transtilla; **16,** labides shaped as narrow sclerotized 'bridges' between juxta and base of transtilla; **17,** labides absent; **18,** waist between tegument and vinculum absent; **19,** muscle *m4* arising from tegumen.

strate high diversity in combination with nonrandom distribution of types in taxa. Among them, labides had been explored as the most phylogenetically informative anellar structure in Geometridae (i.e. applicable for the supporting of many basal nodes in the family). My understanding of the term 'labides' needs to be commented. Because of their high morphological diversity these structures have been named differently in literature (here, only the author is mentioned, who introduced the term, in the historical order): F. Pierce: labides, anellus lobes, furca (part); Th. Albers: Führungsarme; F. Rindge: lateral fold, postero-lateral structures, processes of the anellus, postero-lateral pair of sclerotized areas in manica, lateral ridges; R. Orfila & S. Schajovskoy: canaliculi (incorrect treatment of Pierce's term); J. Holloway: arms of juxta, haired processes from base of valva; W. McGuffin: lobes of juxta; J. Viidalepp: dorsal processes/appendages of juxta; P. McQuillan: lateral/dorsal processes of juxta; A. Hausmann: posterior processes of juxta; L. Pitkin: anellar sclerites. Based on the classic criteria of homology I consider all these structures as homologous and propose the term 'labides' (Pierce 1914) as the senior and most convenient name for them.

The transtilla also provides important apomorphies for basal branching in the Ennominae, but the phylogenetic significance of the transtilla characters can only be realised relative to the attached muscles: dorsal abductor and adductor valvae (*m2* and *m4*, following Kuznetzov & Stekolnikov).

A tentative tribal system of the Ennominae corresponding to the proposed phylogenetic cladogram is represented on the Forum Herbulot website (http://www.zsm.mwn.de/external/herbulot/famgroup2.htm; http://www.herbulot.de).

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