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The structure and musculature of male terminalia in the tribes Eupitheciini, Melanthiini, Perizomini and Rheumapterini: Gnathoi or Agnathoi, that is the question

(Lepidoptera, Geometridae, Larentiinae)

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The skeleton and musculature of the male terminalia were examined and depicted in seven Palaearctic species from the tribes Eupitheciini Pierce, Melanthiini Duponchel, Perizomini Herbulot and Rheumapterini Herbulot (Lepidoptera, Geometridae, Larentiinae) characterized by the presence of the eupitheciine labides in the male genitalia. Nine genital muscles, typical of the subfamily, were identified: m1, m2(10), m3(2), m4, m5(7), m6(5), m7(6), m8(3) and m21. The places of attachment of the muscles m3(2), m4 and m5(7) to the genital sclerites afford useful characters for the higher classification of this group. A few principal genital characters which previously received little attention are discussed, including fusion of the transtilla with parts of the labides and presence of the gnathos in several larentiine tribes.

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Introduction

The application of the characters based on the functional morphology of the male genitalia has provided a large amount of opportunities to solve the phylogenetic problems in Lepidoptera, including the geometrid moths (Kuznetsov & Stekolnikov 2001). Despite thorough taxonomic reviews of the genera assigned to the tribes Eupitheciini, Melanthiini, Perizomini and Rheumapterini (Pierce 1914, Prout 1940, Forbes 1948, McGuffin 1958, Herbulot 1962, Heitzman & Enns 1978, Ferguson 1983, Viidalepp 1977, 1978, 1988, Bolte 1990, McQuillan & Edwards 1996, Holloway 1977, 1997, Scoble 1999, Xue & Zhu 1999, Holloway et al. 2000, Mironov 2000, 2003, Choi 2003, Hausmann & Parra 2009, Leraut 2009), many questions are still not answered. Most recent comprehensive taxonomic, faunistic and morphological studies were completed by Viidalepp (2011)

and Hausmann & Viidalepp (2012). However, the tribal placement of several genera differs in these two studies. Also, modern molecular analyses did not clarify the relationships within the group so far. About a dozen of genera involved in the Eupitheciini complex have been considered in numerous molecular analyses provided 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, Regier et al. 2013). Unfortunately, the data concordance was not achieved concerning the subfamily Larentiinae.

The morphological characters of the tribes are broadly presented by Mironov (2003), Viidalepp (2011) and Hausmann & Viidalepp (2012), therefore the present paper deals mainly with the characters which have received little attention so far. The present study continues the investigation of the male genital musculature of larentiine moths (see Ra-

zowskj & Wojtusiak 1981, Kuznetzov & Stekolnikov 2001, Beljaev 2008, Schmidt 2001, 2013, 2014) and is generally aimed to contribute to the discussion of the relationships among the larentiine moths that belong to a group of tribes, all of them characterized by the presence of the eupitheciine labides in the male genitalia. The eupitheciine labides are defined as arising from the points of union of the transtilla with the costa valvae, having somewhat stalked posterior labides arms partly fused apically, and anterior arms directed towards the lateral margins of the juxta. The present study takes a step towards clarifying the relationships within the eupitheciines and alias based on newly established morphological characters. It is not aimed to provide a full coverage of relationships within the Eupitheciini complex. In the tribes Operophterini Packard and Philereimini Pierce the labides look similar but completely fused to a 'head' apically, whereas in the tribe Asthenini the labides apices are free. These tribes are apparently closely related to the Eupitheciini and alias and will be discussed in a further publication (Schmidt, in prep.). The present study should be considered as part of an integrative approach involving morphology, DNA sequences, ecology and biology which will contribute to resolve the phylogenetic relationships within the subfamily Larentiinae. In addition, the emphasis is placed on the drawing attention to some principal characters, such as the presence of the gnathos in the male genitalia of the larentiine moths.

Material and methods

A total of seven species assigned to four tribes were examined. The material has been collected by O. Schmidt in the following localities: *Eupithecia tantillaria* (Boisduval, 1840) (Germany, Baden-Wuerttemberg, near Stuttgart-Rohr, Glemswald, May 2002); *Gagitodes sagittata* (Fabricius, 1787) (Russia, Primorsky Region, Verkhny Pereval, July 1990); *Horisme vitalbata* (Denis & Schiffermüller, 1775) (Russia, Primorsky Region, Verkhny Pereval, July 1990); *Melanthia procellata* (Denis & Schiffermüller, 1775) (Russia, Primorsky Region, Khasansky district, Kedrovaya Pad Nature Reserve, July 1988); *Mesotype didymata* (Linnaeus, 1758) (Russia, Leningradsky Region, 20 km NW of St. Petersburg, July 1989); *Mesotype verberata* (Scopoli, 1763) (Austria, Tirol, Fernau, Middle Station, July 2003); *Rheumaptera subhastata* (Nolcken, 1870) (Germany, Bavaria, Bayerischer Wald NP, May 2007).

The methods have been described in Schmidt (2013). The images of adult moths are shown in several publications including Xue & Zhu (1999), Ebert (2001), Mironov (2003) and Hausmann & Viidalepp (2012).

Terminology for adult morphology and genitalia follows Pierce (1914), Forbes (1948), Klots (1970), Ni-

chols (1989) and Scoble (1995), with notes on the gnathos (see 'Discussion'). The abbreviations for the sclerites are as follows:

gna	gnathos
jux	juxta
lab	labides
soc	socii
teg	tegumen
tra	transtilla
unc	uncus

Notes on the nomenclature of the musculature are given in Schmidt (2013). The abbreviations are as follows:

m1	depressors of uncus
m2(10)	retractors of anal tube
m3(2)	tergal extensors of valvae
m4	tergal flexors of valvae
m5(7)	flexors of valvae (intravalval muscles)
m6(5)	protractors of aedeagus
m7(6)	retractors of aedeagus
m8(3)	sternal extensors of valvae
m21	retractors of aedeagal vesica (not illustrated)

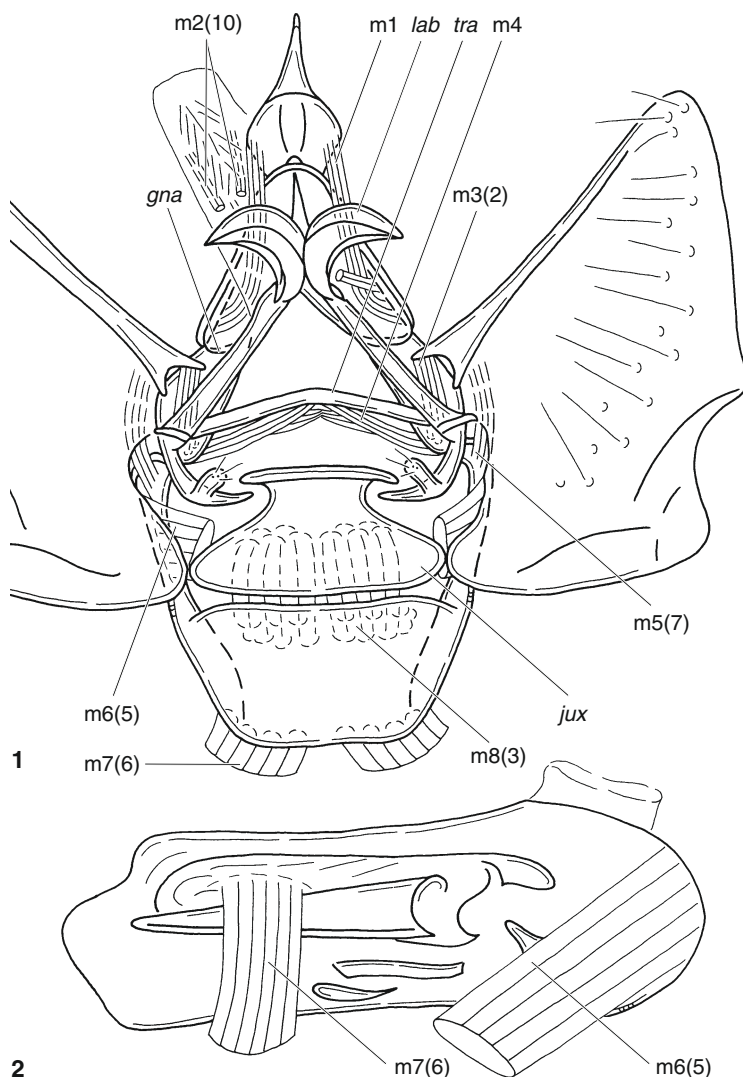
Results

Tribe Eupitheciini

Eupithecia tantillaria

Figs 1–2

The uncus is small and broadened at the base. The narrow ventral band-like sclerotized processes are attached to the base of the uncus laterally, forming a broken medially ring. The band-like processes are apparently homologous to the gnathos arms (see 'Discussion'). The proximal area of the anal tube, including the base of the subscaphium, is connected to the gnathos. The thin muscles m1 extend from the medio-lateral portions of the tegumen to the lateral lobes at the uncus base. The muscles m2(10) are attached to the tegumen, very close to the proximal end of the muscles m1, and run parallel to the subscaphium to the inner surface of the anal tube distally. The basal process of the costa valvae is developed and the muscles m3(2) run to its ventral margin from the proximal portion of the tegumen. The labides arising from the base of the costa valvae ventrally are present. They consist of thin posterior arms bearing setose papillae apically and rather short bent anterior arms with narrow finger-like setose ventral papillae curved towards the juxta laterally. The transtilla arising from the base of costa valvae dorsad of the labides is present as well. The muscles m4, consisting of two almost inseparable bundles, run from the proximal corner of the tegumen to the transtilla medially. The thin muscles m5(7) connect the inner wall of the valva (close to the base of the



Figs 1–2. *Eupithecia tantillaria*, male genitalia and muscles: **1.** Armature (proximal part of subscaphium and middle part of muscles m2(10) not shown). **2.** Aedeagus.

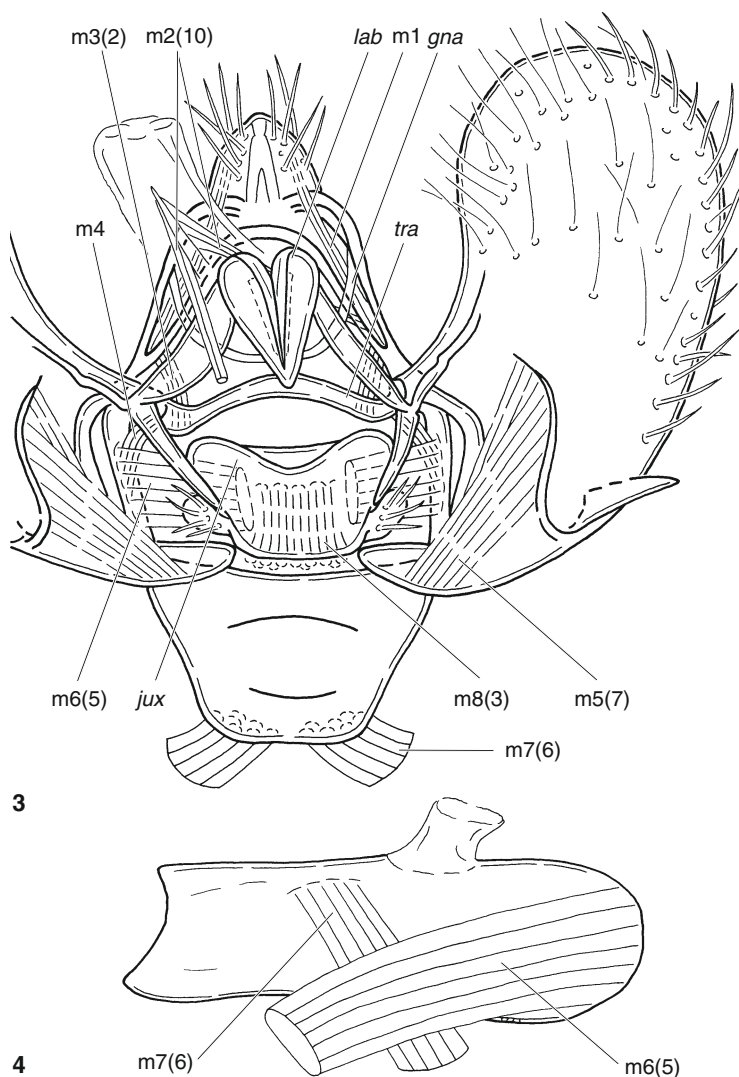
costa valvae) to the vinculum curve. The juxta is rather large, compound, broadest crosswise and placed between the sacculi of the valvae. The voluminous paired muscles m8(3) extend from the posterior margin of the saccus to the posterior area of the juxta. The aedeagus is large, broadest at the basis, with several long and short cornuti of different shape in the aedeagal vesica, with the muscles m6(5) running from the vinculum to the basal process of the aedeagus. The muscles m7(6) connect the large, proximally narrowed saccus to the distal portion of the aedeagus.

Tribe Melanthiini

Melanthia procellata

Figs 3–4

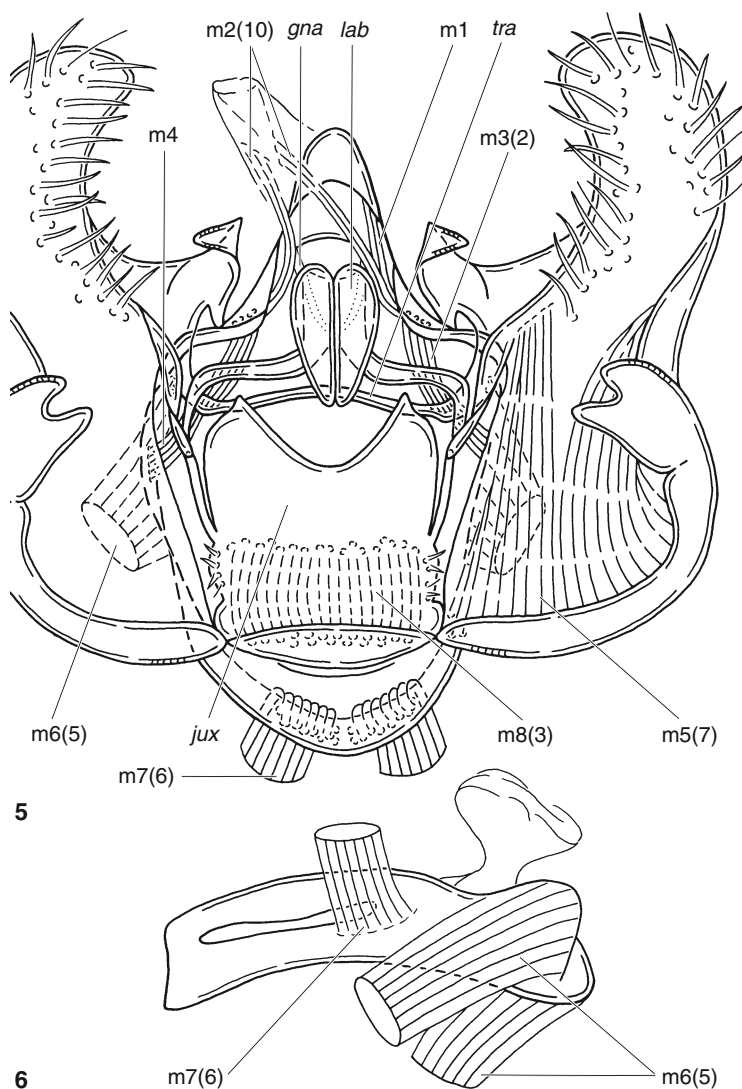
The uncus is much reduced, membranous and covered with setae. The gnathos arms are attached to the base of the uncus laterally, forming a broken medially ring. The tegumen is reduced in size. The proximal area of the medium sized anal tube, including the base of the subscaphium, is connected to the gnathos. The muscles m1 are very thin and



Figs 3–4. *Melanthia procellata*, male genitalia and muscles: 3. Armature (proximal part of subscaphium and muscles m2(10) on the left side not shown). 4. Aedeagus.

run from the lateral portions of the tegumen to the medial area of the uncus, close to the very weakly sclerotized longitudinal suture. The muscles m2(10) extend from the tegumen, near the proximal end of the muscles m1, towards the distal portion of the subscaphium. The relatively broad labides arising from the base of the costa valvae ventrally are present. They consist of the posterior arms bearing setose apical papillae fused to a 'head' medially and thin anterior arms connected to the juxta laterally. The mostly free hanging transtilla arising from the base of the costa valvae dorsad of the labides is also

present, whereby the small pocket-like lateral portions and the medial area of the transtilla are thinly connected to the labides. The muscles m3(2) extend from the lateral portions of the tegumen, ventrad of the muscles m1 and m2(10), to the pocket-like lateral portions of the transtilla. The muscles m4 run from the medial portion of the vinculum to the transtilla laterad of the muscles m3(2), close to the costa valvae. The valvae are relatively broad, with the succulus projected into a fang-like sclerite outwards. The rather powerful muscles m5(7) extend from the medial ridge of the valva to the sacculus,



Figs 5–6. *Horisme vitalbata*, male genitalia and muscles: **5.** Armature (proximal part of subscaphium, muscles m1 and m5(7) on the left side not shown). **6.** Aedeagus.

with a bundle inserted on the vinculum. The juxta is medium-sized, broad heart-shaped, placed between the sacculi of the valvae. The broad muscles m8(3) run from the posterior margin of the saccus towards the posterior margin of the juxta. The aedeagus is large. The powerful muscles m6(5) connect the distal portion of the vinculum to the basal process of the aedeagus. The muscles m7(6) run from the large saccus to the medial portion of the aedeagus.

Horisme vitalbata

Figs 5–6

The uncus is reduced to a crescent-shaped lobe, the anal tube being longer than the uncus. The very fine gnathos arms are attached to the base of the uncus laterally. The tegumen is much reduced in size. The proximal area of the medium sized anal tube, including the base of the subscaphium, is connected to the gnathos. The very thin muscles m1 are attached to the lateral portions of the tegumen and run towards the base of the uncus. The muscles m2(10) extend from

the tegumen, near the proximal end of the muscles m1, and run along the thin subscaphium to the inner surface of the anal tube distally. The narrow labides arising from the base of the costa valvae ventrally are present. As in the *Melanthia* Duponchel, they consist of thin posterior arms bearing setose apical papillae fused to a 'head' medially and thin anterior arms connected to the juxta laterally. The mostly free hanging transtilla arising from the base of the costa valvae dorsad of the labides is similar to *Melanthia* but the connection to the labides is less pronounced. The muscles m3(2) extend from the lateral portions of the tegumen, ventrad of the muscles m1 and m2(10), to the lateral portions of the transtilla. The muscles m4 run from the medio-distal portion of the sclerotized suture of the vinculum to the transtilla laterad of the muscles m3(2). The structure of the valvae is complex, with the succulus bearing a claw-like sclerite distally. The powerful muscles m5(7) extend from the area at the base of the costa valvae and from the medio-ventral portion of the valvae (dorsad of the claw-like sclerite) to the sacculus, with a broad bundle attached to the vinculum. The juxta is large, placed between the sacculi of the valvae. The relatively short and broad muscles m8(3) connect the posterior margin of the saccus to the medial portion of the juxta. The vinculum is sclerotized, with the oblique heavily sclerotized suture in its distal half. The dorsal area of the suture is fused with the very base of the costa valvae. The aedeagus is slightly flattened dorso-ventrally, bearing a cornutus. The location of the powerful muscles m6(5) is rather unusual for the larentiines. They run from the suture on the vinculum, including the area of fusion of the suture with the base of the costa valvae, to the lobes of the basal process of the aedeagus. The muscles m7(6) connect the shallow saccus to the medial portion of the aedeagus.

Tribe Perizomini

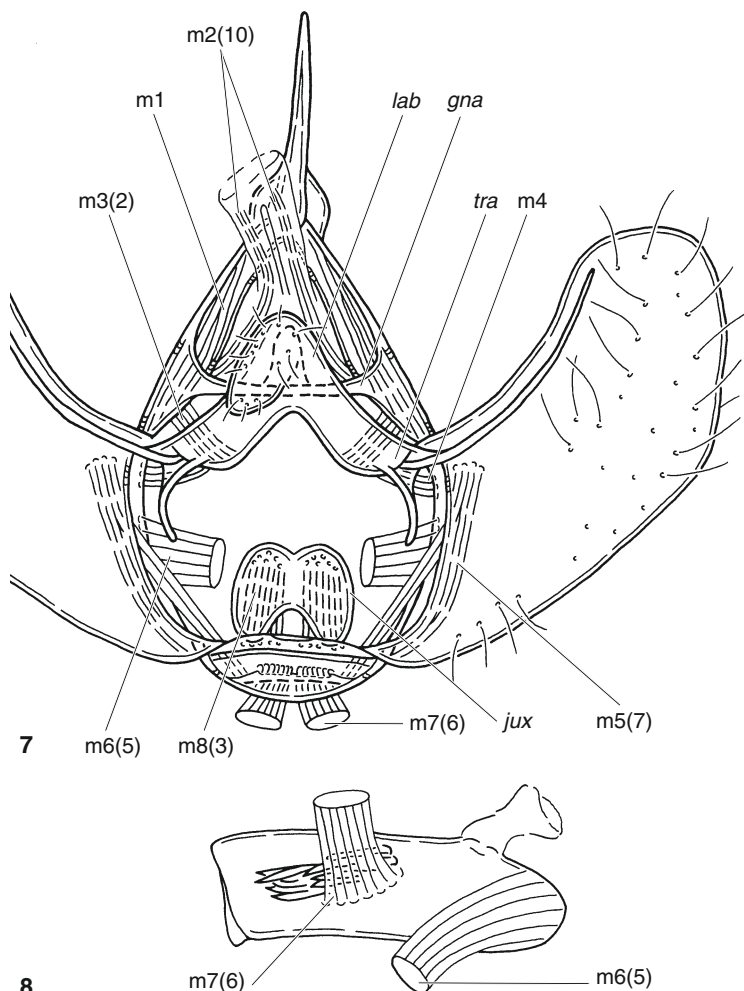
Mesotype didymata Figs 7–8

The uncus is medium-sized, broadened at the base. The gnathos arms are attached to the base of the uncus laterally, forming a broken medially ring. The proximal area of the anal tube, including the base of the subscaphium, is connected to the gnathos. The muscles m1 extend from the lateral portions of the tegumen to the lateral lobes at the base of the uncus. The muscles m2(10) run from the tegumen, dorsad of the muscles m3(2), to the inner surface of the anal tube distally. The transtilla is fused with the broad posterior projections of the labides latero-

medially forming a compound structure, and the muscles m3(2) are attached in the transtilla region. The dorsal end of the muscles m3(2) is attached to the lateral portions of the tegumen. The muscles m4 run from the distal portion of the vinculum to the lateral portion of the transtilla-labides complex. The muscles m3(2) and m4 enable the movement of the valvae and the labides. The relatively thin muscles m5(7) connect the inner wall of the valva (close to the base of the costa valvae) to the not extended sacculus, whereby a small bundle is shifted to the vinculum near the very shallow saccus. The juxta is small, placed between the sacculi of the valvae. The paired muscles m8(3) connect the posterior margin of the saccus to the posterior margin of the juxta. The aedeagus is short and stout, bearing a patch of cornuti, with the muscles m6(5) running from the vinculum ventrad of the muscles m4 to the basal process of the aedeagus. The muscles m7(6) extend from the saccus to the medial portion of the aedeagus.

Mesotype verberata Figs 9–10

The uncus is medium-sized, broadened at the base. The gnathos arms are attached to the base of the uncus laterally. The tegumen is slightly shortened. The proximal area of the anal tube, including the base of the subscaphium, is connected to the gnathos. The relatively thin muscles m1 run from the lateral portions of the tegumen dorsad of the lateral curves of the ring to the base of the uncus laterally. The muscles m2(10) extend from the tegumen, dorsad of the muscles m3(2), to the inner surface of the anal tube distally. As in *M. didymata*, the transtilla is fused with the posterior projections of the labides latero-medially forming a compound structure, and the muscles m3(2) are attached in the transtilla region. The dorsal end of the muscles m3(2) is inserted on the tegumen close to the distal curves of the vinculum. The muscles m4 run from the medio-distal portion of the vinculum to the most lateral portion of the transtilla-labides complex. The muscles m5(7) extend from the inner wall of the valva to the sacculus, with a small bundle shifted to the vinculum. The juxta is medium sized, placed between the sacculi of the valvae. The unpaired muscles m8(3) connect the posterior margin of the not prominent saccus to the posterior region of the juxta. The aedeagus is large, the muscles m6(5) extend from the vinculum ventrad of the muscles m4 to the basal process of the aedeagus. The muscles m7(6) run from the anterior margin of the saccus to the medial portion of the aedeagus.

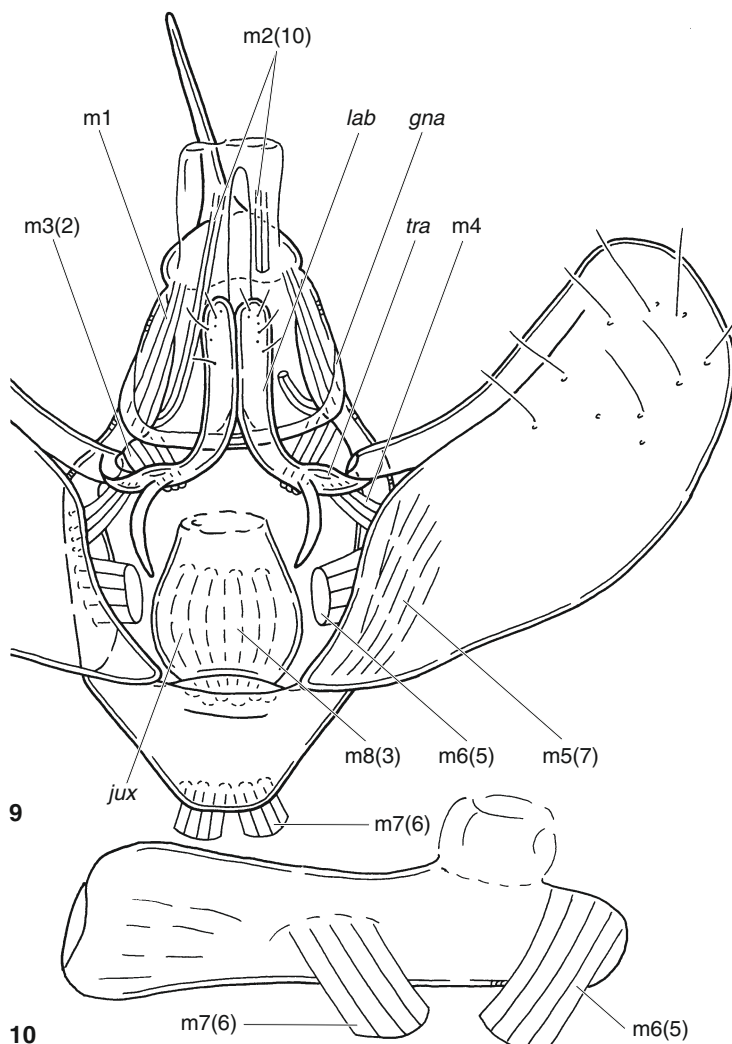


Figs 7–8. *Mesotype didymata*, male genitalia and muscles: 7. Armature (proximal part of subscaphium not shown). 8. Aedeagus.

Gagitodes sagittata
Figs 11–12

The uncus is almost completely reduced, with the setose projections at the base which are presumably homologous with the socii. The short gnathos arms are attached to the base of the uncus laterally. The tegumen is much shortened and rather narrow. The proximal area of the medium sized anal tube, including the base of the subscaphium, is connected to the gnathos. The muscles **m1** were not found. The muscles **m2(10)** run from the tegumen, dorsad of the muscles **m3(2)**, to the inner surface of the anal tube distally, whereby the anal tube resembles an

uncus. As in the genus *Mesotype* Hübner, the transtilla is fused with the broad posterior projections of the labides latero-medially forming a compound structure, and the muscles **m3(2)** are attached in the transtilla region. The thin anterior arms of the labides are fused with the juxta laterally. The dorsal end of the muscles **m3(2)** is inserted on the tegumen. The well developed muscles **m4** extend from the vinculum ventrad of the muscles **m6(5)**. The distal end of the muscles **m4** is attached on the transtilla-labides complex, laterad of the muscles **m3(2)**. The powerful muscles **m5(7)** broadly connect the middle portion of the valva to the sacculus. The juxta is medium sized, placed between the sacculi of the valvae. The



Figs 9–10. *Mesotype verberata*, male genitalia and muscles: **9.** Armature (proximal part of subscaphium, middle part of muscles m2(10) on the right side and muscles m5(7) on the left side not shown). **10.** Aedeagus.

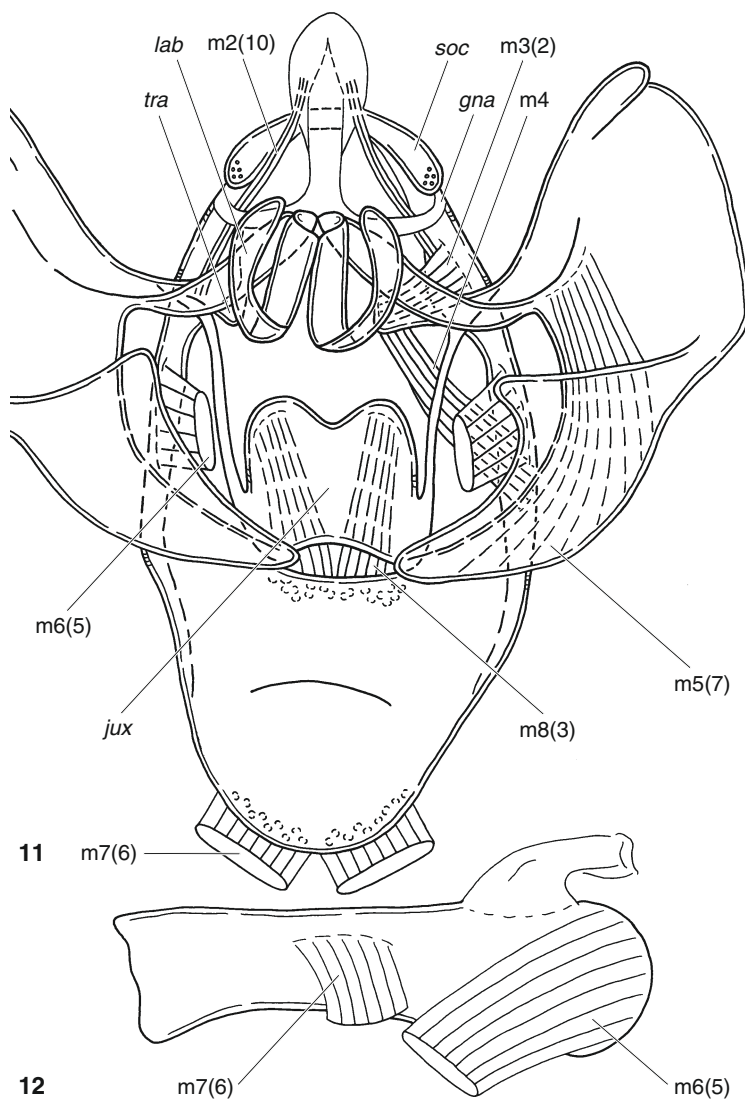
paired muscles m8(3) extend from the posterior margin of the saccus to the curves of the posterior margin of the juxta. The aedeagus is rather large, with the muscles m6(5) running from the vinculum dorsad of the muscles m4 to the basal process of the aedeagus. The powerful muscles m7(6) connect the massive saccus to the medial portion of the aedeagus.

Tribe Rheumapterini

Rheumaptera subhastata

Figs 13–14

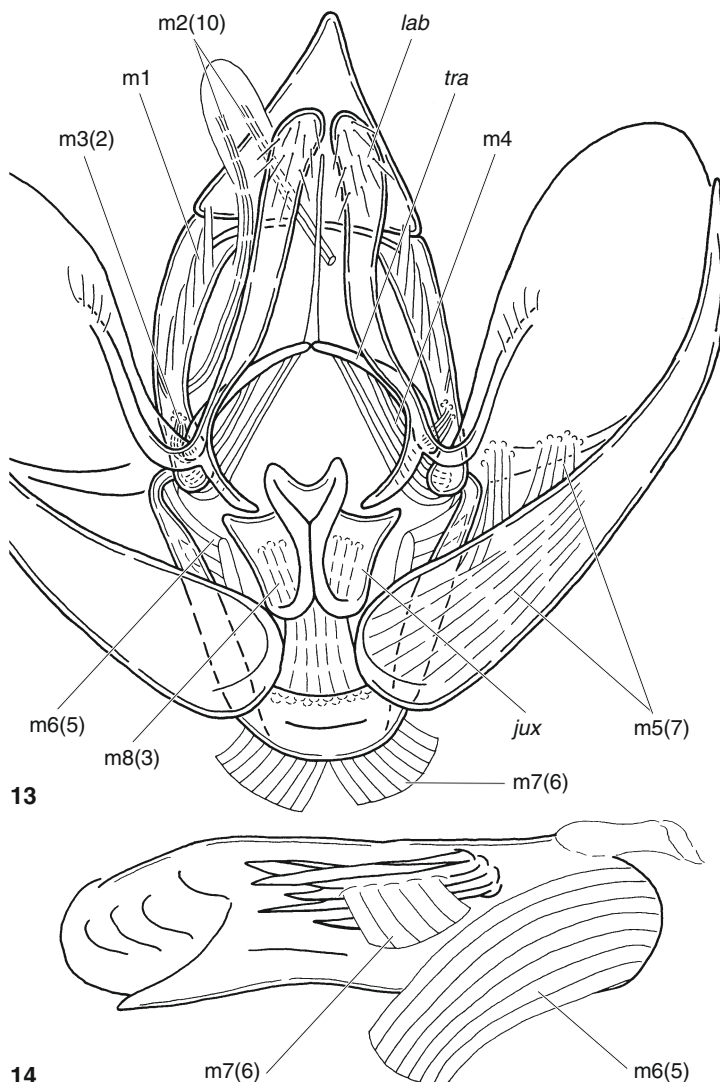
The uncus is slightly flattened dorso-ventrally, shaped like a triangle. The tegumen is not reduced in size, with two sclerotized sutures, and with the muscles m1 running from the tegumen proximally to the lateral portions of the base of the uncus. The muscles m2(10) extend from the tegumen, near the proximal end of the muscles m1, to the inner surface of the anal tube distally. The labides are long, being connected to the medial needle-shaped sclerite by



Figs 11–12. *Gagitodes sagittata*, male genitalia and muscles: **11.** Armature (muscles m3(2), m4 and m5(7) on the left side not shown). **12.** Aedeagus.

a membrane and to the ventral portion of the base of the costa valvae tightly. The proximal portion of the medial needle-shaped sclerite is fused with the transtilla medially. The anterior arms of the labides are short, directed towards the juxta. The arms of the transtilla are placed dorsad of the posterior arms of the labides and are membranously connected to the labides submedially. The slightly twisted muscles m3(2) extend from the tegumen ventrad of the base of the muscles m1 to the most lateral portions of the transtilla. Two inseparable from each other bundles of the muscles m4 run to the medial portions of the

transtilla, originating from the lateral corners of the tegumen, close to the vinculum. In *R. subhastata* the base of the costa valvae is connected to the tegumen, whereas in several related species and in the genus *Hydria* Hübner it is in fact fused with the tegumen. The valval sacculus is projected into a long thick sclerotized spine reaching the valval apex. The powerful muscles m5(7) extend from the area at the base of the costa valvae and from the medial portion of the valvae to the sacculus, with a bundle attached to the vinculum. The juxta is relatively small, shifted towards the tegumen. The muscles m8(3) connect the



Figs 13–14. *Rheumaptera subhastata*, male genitalia and muscles: **13.** Armature (proximal part of subscaphium and muscles m2(10) on the right side and muscles m5(7) on the left side not shown). **14.** Aedeagus.

posterior margin of the shallow saccus to the medial portion of the juxta. The vinculum is relatively narrow and sclerotized. The powerful muscles m6(5) are broadly inserted on the vinculum, with a small bundle being attached to the tegumen, at the area of its connection with the base of the costa valvae (close to the vinculum). The aedeagus is rather large, bearing several distinct cornuti in its vesica. The muscles m6(5) are attached to the basal process of the aedeagus, whereas the muscles m7(6) are inserted on the aedeagus medially and run to the anterior margin of the saccus.

Discussion

The position of the muscles m1, m2(10), m6(5), m7(6), and m21 is similar in all species discussed in the present review, whereby the muscles m8(3) are sometimes paired. The places of attachment of the muscles m3(2), m4 and m5(7) to the genital sclerites afford useful characters for the higher classification of this group.

The fusion of the transtilla with different parts of the labides is characteristic of the tribes Melanthiini, Perizomini, Rheumapterini and of several other

related tribes not included in the present analysis (Schmidt, in prep.), whereby the fusion is well pronounced in Perizomini and the muscles m3(2) and m4 enable the movement of the valvae and the labides. It is worth noting that in most of the larentiine tribes discussed earlier the muscles m3(2) and m4 were associated with the basal process of the costa valvae, the transtilla, or with the juxta (see Schmidt 2001, 2013, 2014) and not directly involved in the movement of the labides.

The more lateral position of the muscles m4 compared to the muscles m3(2) is characteristic of the perizomines and melanthiines.

The absence of the coremata on the eighth abdominal segment is shared by Eupitheciini and Rheumapterini.

The gnathos arms are distinct in all tribes except Rheumapterini.

Tribe Eupitheciini

The transtilla is not fused with the labides. In contrast to other tribes discussed here, the costa valvae is produced in a short basal processes, and the muscles m3(2) are inserted on it. The muscles m4 run from the tegumen and are attached to the transtilla medially, as in the rheumapterine moths. The valvae are rather thin and the muscles m5(7) are weaker than in other tribes.

As in the Rheumapterini, a pair of coremata pockets on the eighth abdominal segment laterally and the octavals on the eighth segment ventrally are present.

Remarks. The male genital musculature of *Eupithecia succenturiata* (Linnaeus, 1758) and of *E. plumbeolata* (Haworth, 1809) has been examined by Razowski & Wojtusiak (1981) and by Valersky (2011) respectively.

Tribe Melanthiini

The transtilla is partly fused with the labides but the connection is rather flexible. The muscles m3(2) are attached to the transtilla medially of the muscles m4, whereas in the rheumapterines the muscles m3(2) are inserted laterad of the m4. The absence of the muscles m3(2) at the base of the costa valvae is shared with the tribes Perizomini and Rheumapterini. The muscles m6(5) usually run from the suture on the vinculum, including the area of fusion of the suture to the base of the costa valvae.

Although the structure of the male genitalia in the genera *Melanthia* and *Horisme* is very similar, the attachment of the muscles m1, m5(7) and m6(5) differs. This can be explained by the reduction of the

uncus and the presence of a small bent sclerotised projection at the base of the costa valvae in *H. vit-albata*.

In *Horisme* the muscles m6(5) are broadly inserted on the vinculum, with a distal bundle being attached to the suture at the base of the costa valvae. The attachment of the muscles m6(5) to the valvae is supposed to be a plesiomorphic character (Hannemann 1957, Kuznetsov & Stekolnikov 2001). However, in the melanthiines the position of these muscles appears to be secondary and can be explained by the modification of the base of the costa valvae.

The coremata on the eighth abdominal segment and the octavals are absent.

Remarks. Attachment of the muscles m6(5) to the vinculum and partly to the valvae in the male genital musculature of *Horisme tersata* (Denis & Schiffermüller, 1775) was pointed out by Kuznetsov & Stekolnikov (2001), whereby *H. tersata* was treated as a rheumapterine species. The musculature of *M. procellata* has been briefly discussed by Kuznetsov & Stekolnikov (2001), whereby the genus has also been associated with the tribe Rheumapterini.

Valersky (2011) described the melanthiine male genital musculature based on the species *Anticollix sparsata* (Treitschke, 1828). Association of this species with the tribe Melanthiini is questionable (see also Hausmann & Viidalepp 2012).

Tribe Perizomini

The transtilla is fused with the posterior projections of the labides latero-medially, forming a compound transtilla-labides structure. The muscles m1 are developed to a different extent, apparently corresponding to the degree of sclerotization of the uncus. The muscles m3(2) and m4 are inserted closer to the dorsal portion of the compound structure corresponding to the transtilla (the muscles m4 are attached more laterally).

The coremata on the eighth abdominal segment and the octavals are absent.

Remarks. The material obtained for the present study allowed discussion of the genera *Mesotype* and *Gagitodes*. The male genital musculature of the type species *Perizoma albulata* (Denis & Schiffermüller, 1775) has been illustrated by Valersky (2011) who considered that the muscles m3(2) were running from the tegumen to the medial region of the transtilla and the muscles m4 were running from the genital segment in the area of the attachment of the valvae to the lateral parts of the transtilla. However, the given illustration (Valersky 2011, fig. 14) does not support his apparently erroneous statement. The muscles

m3(2) seem to be inserted on the lateral region of the sclerite looking like the transtilla, and the muscles m4 seem to extend from the distal portions of the vinculum. The morphology of the transtilla and the labides has not been discussed by Valersky (2011). Nonetheless, the illustration of *P. albulata* indicates the fusion of the transtilla with the posterior projections of the labides.

Tribe Rheumapterini (sensu Viidalepp 2011)

The transtilla is weakly connected to the base of the costa valvae laterally and has a connection with the labides submedially. In contrast to the other tribes, the gnathos is not pronounced. The homology of the sclerotized regions at the base of the uncus and along the lateral margins of the tegumen with the gnathos arms is suggested but needs to be tested. The muscles m4 run from the tegumen and are attached to the transtilla medially, as in the eupitheciine moths but with a small gap between the left and the right bundles. The muscles m6(5) are inserted on the vinculum, with a small bundle being attached to the tegumen at the area of its connection with the base of the costa valvae. The peculiarity of the location of these muscles can be explained by the connection of the base of the costa valvae to the tegumen.

The close relationship of the Melanthiini and Rheumapterini suggested by Herbulot (1962) has not been confirmed. The structure and position of the labides and juxta, the shape of the sacculi and the location of the muscles m4 show considerable differences.

As in the Eupitheciini, a pair of small coremata pockets at the eighth abdominal segment and the weakly sclerotized octavals on the eighth segment ventrally are present.

In several publications the genera *Triphosa* Stephens and *Pareulype* Herbulot were placed in Rheumapterini (e.g. Viidalepp 1996, Forum Herbulot 2003), although they were also mentioned, together with the *Strepsizuga* Warren and *Speluncaris* Bruand which are treated as synonyms of *Triphosa* (Scoble 1999), in the tribe Triphosini (see Viidalepp 2011). Currently, *Triphosa* and *Pareulype* are assigned to the Rheumapterini (Hausmann & Viidalepp 2012, Karsholt et al. 2013). A preliminary study of the morphology revealed that these two genera do not share several characters listed for Rheumapterini. The male genital structure and musculature of *Triphosa* and *Pareulype* await an examination, and the tribal assignment of these genera needs additional discussion (Schmidt, in prep.).

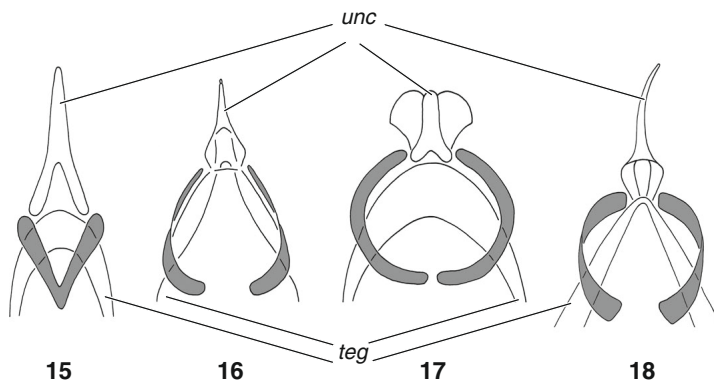
Remarks. The male genital musculature of *Hydria undulata* (Linnaeus, 1758) has been examined by Valersky (2011).

Notes on the gnathos

The loss of the gnathos in the larentiine male genitalia, except for some genera of the tribe Trichopterygini, is generally considered (e.g. Pierce 1914, Craw 1986, Viidalepp 1990, 2011, Holloway 1997, Han et al. 2010, Rajaei et al. 2011, Li et al. 2012, Hausmann & Viidalepp 2012). Pierce (1914) stressed the importance of the gnathos in the male genitalia of geometrid moths and split the Geometridae into two divisions, Gnathoi and Agnathoi, whereby he assigned all the larentiine moths, including “Lobophorinae” (Trichopterygini and several other genera) into Agnathoi. Hundred years later this opinion needs a revision.

In recent decades the term ‘gnathos’ has been used only in a few studies considering non-trichopterygine larentiine genera. Mentzer (1981) and Hausmann & Viidalepp (2012) suggested the homology of the sclerites attached to the uncus base and directed towards the valve in *Docirava* Walker (Chesiadini) with a broken gnathos. Additionally, considering the figures in Hausmann & Viidalepp (2012), other Chesiadini seem to have a weak gnathos. Han et al. (2010) pointed out that the genera *Laciniodes* Warren and *Pseudostegania* Butler, with still uncertain tribal status, shared a remarkable feature, namely the presence of the gnathos. Beljaev (2008) illustrated the gnathos of *Solitanea defricata* (Püngeler, 1904) (Solitaneini). Craw (1986) mentioned the gnathos arms in *Aponotoreas anthracias* (Meyrick, 1883) tentatively placed in the tribe Hydriomenini. Unfortunately, no further discussions were presented. Describing a new species of *Eupithecia* from South Africa, Krüger (2007) used a term ‘pseudognathos’ for the sclerite ventrad of the base of uncus, without further explanation. The results of the current study indicate that the sclerotized arms attached to the base of the uncus laterally in the tribe Eupitheciini and allies are homologous to the gnathos (Figs 15–18).

The term ‘gnathos’ was introduced by Pierce (1914). Klots (1970) defines this structure as a band-like process attached to the caudal margin of the tegumen on each side ventrad of the uncus, enclosing the anal tube, whereby the anal tube may be more or less fused with a gnathos, forming a confusing complex. According to Klots (1970) and Kristensen (2003), the subscaphium is a weak, medial, sometimes setose sclerotization on the ventral surface of the anal tube. The current study revealed that in the eupitheciines and allies the proximal area of the



Figs 15–18. Male genitalia, dorsal sclerites: 15. *Idaea* sp. 16. *Eupithecia* sp. 17. *Melanthia* sp. 18. *Perizoma* sp.; Gnathos is displayed in grey.

anal tube is connected to the gnathos arms which are usually not well pronounced and weakly sclerotized. The gnathos arms are shaped like longitudinal areas of sclerotization along the lateral margins of the apical part of the tegumen. In contrast, in the genera with well pronounced, ‘hanging’ gnathos which is usually articulated with the base of the uncus laterally, the lateral margins of the tegumen are evenly sclerotized, sometimes with a very thin, darker edge. In most lepidopteran taxa, particularly in the geometrid moths, there is no muscle attachment on the gnathos. In the eupitheciines and allies, the musculature in this region is absent as well.

Having studied the skeleton and musculature of the male genitalia in the geometrid moths, including several presumably primitive gnathos-bearing genera of the larentiine tribe Trichopterygini, Beljaev (2008) suggested the connection of the subscaphium of the anal tube to the gnathos a synapomorphy for the subfamilies Larentiinae and Sterrhinae. He noticed that this character might be not applicable for the species with the gnathos reduced.

While investigating the morphology of the male genitalia in *Eupithecia*, Vojnits (1987) made an attempt to describe a “peculiar organ unknown elsewhere in the order Lepidoptera, but here characterising a whole taxonomic group”. He mentioned “the two lateral, sclerotized arcs” fused medially and attached to the tegumen. The results from the present study show that the “peculiar organ” is apparently a gnathos, and this sclerite is not unique to the Eupitheciini.

Interestingly, the remnants of the gnathos arms were found in the male genitalia of various larentiine tribes (Schmidt, unpubl. data). It appears that the gnathos is not lost in the larentiine male genitalia and awaits further studies in the subfamily. In addition, the cases of the absence of the gnathos in several species from other geometrid moth subfamilies should be examined.

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Buchbesprechungen

7. Zetterström, Dan, Ottosson, Mats & Barthel, Peter H. 2014. Kosmos Vogeljahr 2015. – Franckh-Kosmos Verlag, Stuttgart, 105 Farbzeichnungen, 160 Seiten, laminierter Pappband. ISBN 978-3440144732.

Der wie auch sein Vorgänger ansprechend und hochwertig gemachte Buchkalender wird bei seinen Nutzern wieder viel Freude auslösen. Insbesondere durch die gediegene Aufmachung mit Goldschrift und sehr gut für Eintragungen geeignetes Papier nimmt man das kleine Werk gerne zur Hand. Der vogelkundlich Interessierte wird sich aber vor allem an den 105 Farbzeichnungen von Dan Zetterström erfreuen. Am Rand jeder wöchentlichen Doppelseite sind Informationen zu einigen der jeweils jahreszeitlich interessanten heimischen Vögel zu finden. Hierbei wird Wert auf die verhaltensbiologischen und phänologischen Eigenschaften und das Auftreten der Arten gelegt und nicht so sehr auf deren morphologische Merkmale. Zu Monatsbeginn findet sich eine Seite mit aktuellen Zusatzinformationen mit einem Aquarellbild. Der Kalender lässt in seinen Tagesspalten Platz für die Eintragung von Beobachtungsvermerken, Wettersymbole ermöglichen das Festhalten der meteorologischen Situation. Für den Rucksack eigentlich zu schade, wird "Kosmos Vogeljahr 2015" mit seinen nützlichen Informationen für Vogel- und Buchliebhaber und gleichzeitig als kunstvolles Buch eine Bereicherung sein und das Eintragen von Vögelerslebnissen zu einer überaus nützlichen Gewohnheit werden. Man freut sich schon auf den nächsten Jahresband.

Manfred Siering

8. Mebs, Theodor & Schmidt, Daniel 2014. Die Greifvögel Europas, Nordafrikas und Vorderasiens. Biologie, Kennzeichen, Bestände. – Kosmos Verlag, Stuttgart, 2. Auflage, 496 Seiten, 389 Farbfotos, 346 Farbzeichnungen, 46 SW-Zeichnungen, laminierter Pappband, 28 x 21 cm. ISBN 978-3-440-14470-1.

Alle 45 Arten Europas, Nordafrikas und Vorderasiens u.a. mit aktualisierten Bestandszahlen (die Erstauflage war 2006, bei gleicher Seitenzahl, rezensiert im Ornithologischen Anzeiger 45, S. 93 f.) werden in dem opulent gemachten Band behandelt. Das großartige, aber auch gewichtige Handbuch mit rund 800 ausgewählten Fotos und naturgetreuen Zeichnungen beschreibt ausführlich Biologie, Verhaltensweisen, Anpassungen, Lebensraum-Ansprüche und Schutzbemühungen. Alle 45 in der Westpaläarktis als Brutvögel vorkommenden Greifvögel werden mit aktualisierten Bestandszahlen auf bis zu zwölf Seiten pro Art vorgestellt. Greifvögel faszinieren nicht nur die Ornithologen von jeher – vor allem durch ihren eindrucksvollen Flug, ihre vielfach rasante Jagdweise, eine spannende Biologie und ihre Stellung oftmals an der Spitze der Nahrungspyramide. In der neu gefassten Einleitung tragen die Autoren auch gleich der Änderung der Systematik insofern Rechnung, als sie darauf hinweisen, dass es sich bei den Vogelgruppen der Greif-

vögel und Falken um zwei voneinander unabhängige Ordnungen handelt, die in der Systematik gleichrangig nebeneinander stehen. Im Vorwort zur 2. Auflage werden als Rückgangsursachen für die Bestände einiger Arten der zunehmende Anbau von Mais und der Verlust von artenreichem, extensiv bewirtschaftetem Grünland angeführt, wovon z. B. Rotmilan und Schreiadler erheblich schlechtere Überlebensbedingungen haben. Bei der Abhandlung der Lebensrisiken von Greifvögeln und Falken werden bereits im allgemeinen Teil die Negativfaktoren wie illegale Aushorstung, Fallen, Giftköder, Blei- und Vergiftungsopfer, Diclofenac, Anprall an Glasfassaden, Buswartehäuschen, ungesicherte Stromleitungsmasten und Anflug an Leiterseile, der Straßen- und Schienenverkehr und der zunehmende Tod an Windenergieanlagen erwähnt. Auch in seiner 2. Auflage vermittelt dieses umfassende Werk einen reichen Wissensfundus und Argumente der Ornithologen und Vogelschützer für eine der faszinierendsten Tiergruppen unserer Erde.

Manfred Siering

9. Schmidt, Thomas 2012. Entdecke die Zugvögel. – Natur und Tier-Verlag, Münster, 48 Seiten, durchgehend Farbfotos, Großformat 20,7 x 28 cm, Hardcover. ISBN 978-3-86659-214-8.

Das ansprechend aufgemachte und reich bebilderte Buch bietet viele spannende, kindgerecht aufbereitete Informationen über den Vogelzug. Wie ist er entstanden? Wie wird er erforscht? Wie läuft er im Einzelnen ab, und wie orientieren sich die Zugvögel? Welchen Gefahren sind sie ausgesetzt? Wo und wann können Kinder Zugvögel gut beobachten und bestimmen? Das preiswerte und mit vielen eindrucksvollen Farbfotos in geschicktem Layout versehene Bilderbuch wendet sich vornehmlich an Kinder und Jugendliche. Im Winter sind Schwalbe, Storch & Co. plötzlich verschwunden. Wohin sind sie geflogen, und aus welchem Grund bleiben sie nicht einfach hier? Vögel sind Wanderer zwischen Ländern und Kontinenten. Manche legen riesige Strecken zurück. Viel Spannendes rund um die Zugvögel gilt es zu entdecken: Warum wandern sie fort? Wie schaffen Zugvögel ihre beschwerliche Reise? Mit welchen Methoden untersuchen Forscher den Vogelzug? Wie finden Nachtzieher ihren Weg in der Dunkelheit? Diese und alle anderen Fragen zu den Wanderern der Lüfte werden hier in verständlicher Form beantwortet – eine kurzweilige Entdeckungsreise durch die aufregende Welt der Zugvögel! Langstreckenzieher und Kurzstreckenzieher. Welche Zugvögel leben bei uns? Gefahren für Zugvögel. Extra: Langstreckenzieher Weißstorch. Extra: Großes Zugvogelquiz. Extra: 20 tolle Sticker. Antworten auf alle ihre Fragen finden wissensdurstige junge Naturforscher in diesem unterhaltsam geschriebenen Buch! Insgesamt eine informative und preiswerte Einsteighilfe für junge Vogelkundler.

Manfred Siering

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