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Article

On the terminology of the genitalia structures of lichen moths (Lepidoptera: Erebidae: Arctiinae: Lithosiini) with some references to Noctuidae

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Abstract
The present paper briefly describes the Lithosiini genitalia and discusses their terminology. Twelve new terms are introduced: *medius*, *introrsum*, *conjuga*, *collis*, *iuba*, *jugum basalis*, *jugum distalis*, *arcus*, *intersaccular bridge*, *lamella centralis*, *clasper region*, and *elasma* for the male genitalia, and *diverticulum bursae* for the female genitalia. The terminological inconsistencies in Noctuidae are discussed with reference to the original concept by the various authors who introduced the terms, and the approaches by authors *sensu auct.* are also considered. In cases of discrepancies the terms preferable are suggested. Fully annotated figures are provided for the structures discussed.

Key words ampulla, clasper, clasper region, collis, conjuga, diverticulum bursae, editum, elasma, harpe, intersaccular bridge, introrsum, iuba, jugum basalis, jugum distalis, medius, lamella centralis, Noctuoidea, tendon, transtilla, pollex, processus momenti, valvella, valvula.

Introduction

The well-established terminology is an essential tool for taxonomic and phylogenetic studies based on the morphology of organisms, and this statement is fully applicable to lichen (footman) moths (Arctiinae: Lithosiini) which display complex and diverse morphology of the external and internal genitalia. In past publications devoted to the taxonomy of this species-rich group of Lepidoptera, various authors have followed different terminologies, which have sometimes made morphological treatments confusing. Birket-Smith (1965) made an attempt to introduce a special terminology for Lithosiini genitalia based on the Afrotropical and some Palaearctic and Oriental taxa of the subtribe Lithosiina examined by him. However, Birket-Smith's terminology was not widely used in most of the subsequent publications since then as it is hardly applicable to other, morphologically distinct subtribes (e.g., Bendib & Minet 1999; Holloway 2001; Scott & Branham 2012). The prevailing concept has become the use of the basic terminology accepted for Noctuidae and Erebidae, as a result of the downgrading of the family Arctiidae to a subfamily within the family Erebidae based on molecular phylogenetic analyses

(Lafontaine & Schmidt 2010; Zahiri *et al.* 2011, 2012; Witt *et al.* 2011). The Noctuidae and Erebidae terminology, however, is also confusing in a number of aspects as homologous structures are referred to in different ways depending on the authors or the same terms are used to refer to different, non-homologous structures. Additionally, some of the structures found in the Lithosiini genitalia have no designated terms in the Noctuidae and Erebidae terminology, which makes preparation of descriptions and diagnoses problematic.

The present paper is an attempt to put the terminology of the Lithosiini genitalia in order. It is based on the general Lepidoptera terminology (Pierce 1909; Forbes 1939; Klots 1970; Kuznetzov & Stekolnikov 2001; Kristensen 2003a) applied to Noctuidae and Erebidae (Sukhareva 1973; Fibiger 1997; Goater *et al.* 2003; Hacker 2004; Fibiger & Hacker 2007; Fibiger *et al.* 2009; Kononenko 2010), and updated with some terms introduced by Birket-Smith (1965). As there were no terms applicable for certain structures, a number of descriptive names are suggested and twelve new terms (indicated as 'nom. nov.') are also introduced below. As the current Noctuidae terminology of different authors was found controversial in a number of cases, the present paper also contains a discussion of a few Noctuidae terms in order to clarify the terminological inconsistencies.

Material and methods

Abbreviations of the depositories used: ANHRT = African Natural History Research Trust (Leominster, United Kingdom); CAV = research collection of Anton Volynkin (Leominster, United Kingdom); MWM/ZSM = Museum Witt Munich in the Bavarian State Collection of Zoology (Museum Witt München / Zoologische Staatssammlung München, Munich, Germany); NHMUK (formerly BMNH) = Natural History Museum (London, United Kingdom); OUMNH = Oxford University Museum of Natural History (Oxford, United Kingdom).

The genitalia were dissected and embedded in Euparal on microscope slides. The photographs of the genitalia preparations were taken using a Nikon D3100/AF-S camera attached to a microscope with an LM-scope adapter. All photographs were processed using the Adobe Photoshop CC 2018 software.

Results

Although some muscles are mentioned below in order to explain the function and homology of some structures, it is not the main aim of this present paper to characterise the musculature of the genitalia, the detailed information of which can be found in the relevant works (e.g., Forbes 1939; Birket-Smith 1965; Kuznetzov & Stekolnikov 2001; Kristensen 2003a).

Male genitalia

The male copulatory apparatus of Lithosiini consists of the derivatives of the 9th and 10th abdominal segments. The 11th segment is reduced, and its putative derivatives are found only in some Microlepidoptera families (Kristensen 2003a), but not in Lithosiini.

For reasons of convenience, it is generally accepted to remove the phallus from the annulus-valvae-uncus complex during the dissection process and examine and illustrate them separately, and this complex is frequently referred to in the literature as the ***genital capsule*** or *clasping apparatus*.

The 9th abdominal segment

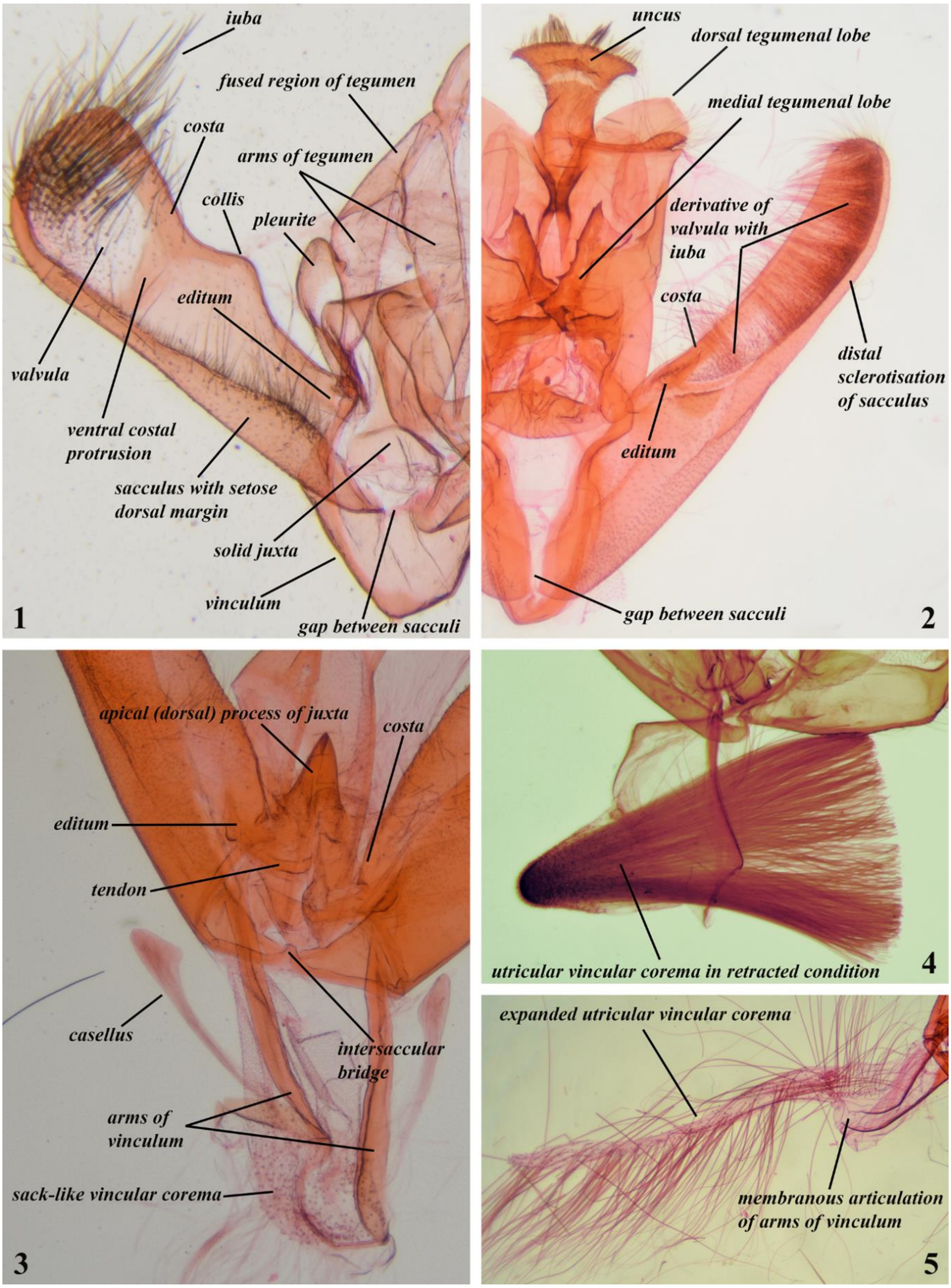
In Lepidoptera the 9th abdominal segment is transformed into a sclerotised ring called the ***annulus*** and consists of a dorsal part, the ***tegumen*** and a ventral ***vinculum***, which are homologous with the 9th tergum and sternum, respectively. In Lithosiini, there is a secondary articulation between these sclerites formed by lateral thinning, and in some groups a ***pleural sclerite*** (or ***pleurite***) is also present (Figs 1, 11, 12, 17). The annulus has sometimes been referred to in the literature as a 'tegumen-vinculum complex' (e.g., Lödl 2000; Durante & Zangrilli 2016; Volynkin & Černý 2021) and serves as an insertion point for several groups of muscles (Forbes 1939; Birket-Smith 1965).

The ***tegumen*** is weakly sclerotised (more rarely, heavily sclerotised), and consists of two ***arms***, which can be relatively narrow or strongly dilated dorsally. In the latter case the cranial (anterior) margins of the arms can be fused dorsally and in certain genera the fused area can occupy up to 4/5 of the arm lengths, which makes the whole structure capsule-like with a dorsal section being downcurved (e.g., Figs 11, 14, 19, 25, 32, 34). In a few genera, the caudal (posterior) margins of the tegumen bear sclerotised ***tegumenal lobes*** medially or dorsally (Figs 2, 39), which do not bear setae and are apparently not homologous with the weakly sclerotised setose tegumenal formation called the *peniculus* (Pierce 1909), which is present in a number of groups in Noctuidae.

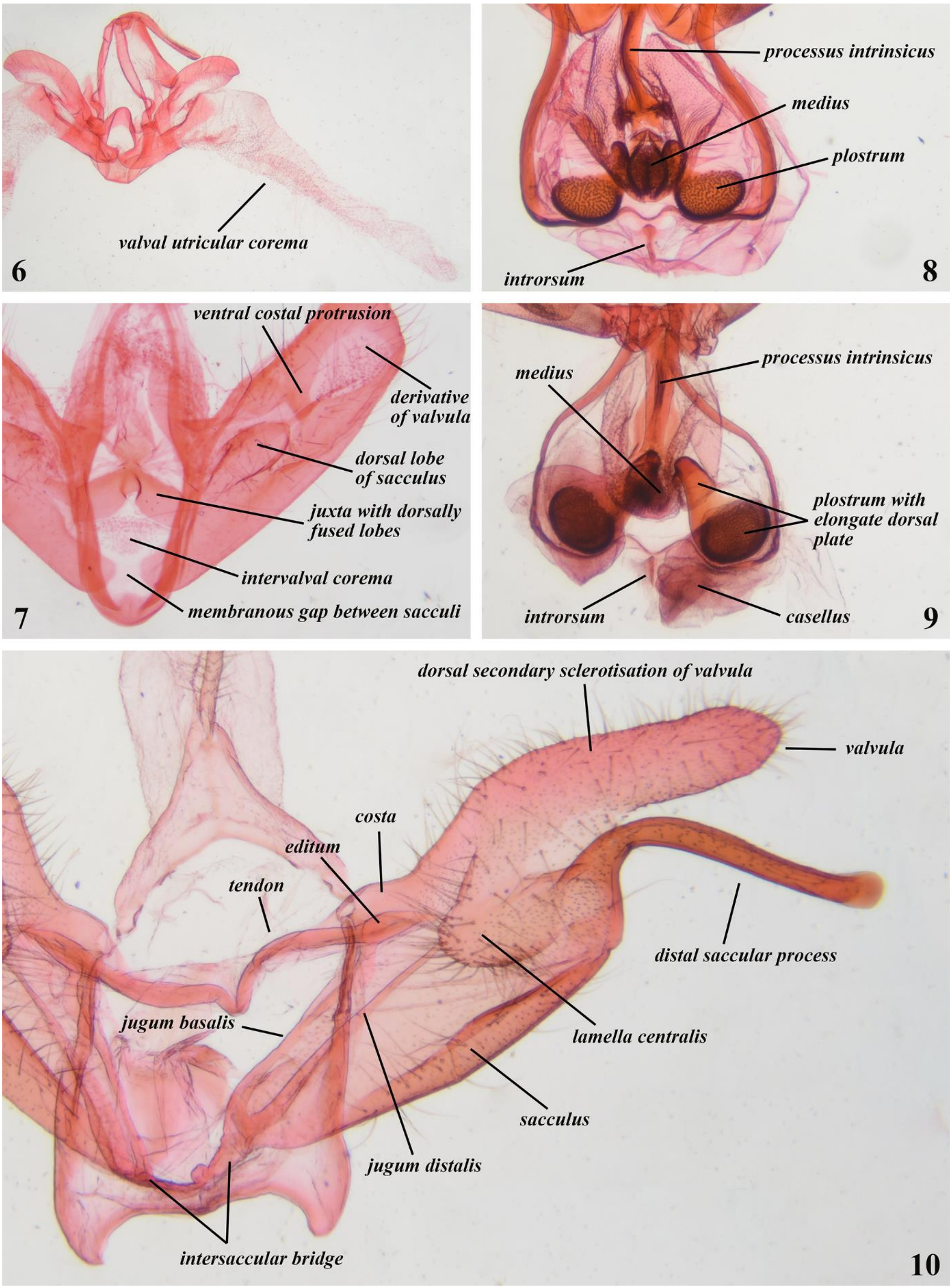
The ***vinculum*** of Lithosiini is diverse in its length, shape and degree of sclerotisation. In some groups it bears a ventral enlargement directed anteriorly (cranially), which is termed the ***saccus*** (Fig. 22). In certain genera of the subtribe Lithosiina the vinculum is strongly elongate, has thin arms (Figs 3, 8, 9, 11), and sometimes bears a thin and weakly sclerotised ventral end (in extreme cases the lateral arms are ventrally connected via a membrane) (Fig. 5). The ***intravincular area*** in Lithosiina may bear various structures such as ***coremata*** (singular: ***corema***) and secondary sclerotisations. The coremata are membranous and eversible structures bearing long hair-like androconial macrochaetes that release pheromones (Boppré & Schneider 1989; Birch *et al.* 1990; Kristensen 2003a), and in Lithosiini they can be paired or single. The shape of the eversible membranous base of the ***intravincular corema*** varies from a short but broad sack (Fig. 3) to a strongly elongate and narrow utricular structure evenly covered with macrochaetes along its length (Fig. 5). In the case of the latter when it is retracted (Fig. 4) inwards, it is reminiscent of a *hairpencil* (and was incorrectly called this by Krüger (2015)), known in various groups of Noctuoidea, which is a functionally similar but morphologically different structure having a sclerotised base (a *lever*) and being forced out of its pocket-like chamber with the help of muscles as opposed to coremata being inflated with air (Birch *et al.* 1990). In certain Asiatic species of *Siccia* Walker, 1854 *s.l.* a long utricular corema bearing short and thin hairs is present on the outer surface of the valva (Fig. 6). The similar ***valval coremata*** are known in the Arctiini genus *Amerila* Walker, 1855 (Bethune-Baker 1925; Holloway 1988; Häuser & Boppré 1997). In other subtribes of Lithosiini the coremata are also frequently present in the intervalval membrane ventrally from the juxta (Fig. 7) or in the abdomen, not genitalia (see Holloway 2001).

Secondary intravincular sclerotisations are found in the Lithosiina genus *Teulisna* Walker, 1862 (Figs 8, 9), some of them probably serving as insertion points for some muscles but the vincular musculature of this group has never been studied in detail. Holloway (2001) called these sclerotisations as ‘structures’ despite Birket-Smith (1965) having already introduced names for some of them, which are suggested herein for prevailing usage while new names for the others are introduced in the present paper. The ***processus intrinsicus*** (Birket-Smith 1965) is the sclerotised rod-like medial sclerite stretching longitudinally from the intersaccular bridge (see below) to the middle of the intravincular area, and can be ventrally dilated. The ***medius*** (nom. nov.) is a sclerotised plate situated ventrad of the ventral dilated end of the processus intrinsicus and articulated with it via a membrane. Ventro-lateral margins of the medius are firmly articulated with the dorsal protrusions of the plostri. The ***plostrum*** (pl.: *plostri*; Birket-Smith (1965): as plostrae) is a paired sclerotised formation in the ventral region of the intravincular area, which is ventrally articulated with the vinculum margin. It consists of a flat dorsal plate connected to the medius and a dorsal rounded, elliptical or bean-shaped swollen enlargement with a cellular surface. The lateral and ventral parts of the intravincular membrane of *Teulisna* are extended and sack-like, protruding cranially (anteriorly). The ventral wall of this sack bears a short and slender longitudinal sclerotised plate articulated with the ventral end of the vinculum via an area of weak sclerotisation. It is suggested herein to term this sclerite as the ***introrsum*** (nom. nov.).

The plostrum bears a sack-like, gelatinous, and easily detachable body termed by Birket-Smith (1965) as the ***casellus*** (pl.: caselli) (Fig. 8). Birket-Smith (1965) described caselli as “lumps, which are in sections appear as a homogenous proteineous substance with an irregular cellular structure”. The function of this structure is unclear and requires further studies, with similar paired vincular gelatinous processes also known in certain other genera (e.g., in *Manulea* Wallengren, 1863 and *Collita* Moore, 1878) (Fig. 3). Despite these gelatinous processes originating from the membranous wall of the intravincular coremata, not the sclerotised plostra, it is suggested herein to use the same term caselli to refer to them until the homology of the structures is studied. In this case the proximal section of the casellus is strongly elongate and pole-like while its tip is flattened and fan-like.



Figures 1–5. Details of the male genitalia structures of Lithosiini. 1, *Miltochrista* Hübner, [1819], slide ZSM Arct. 2019-1018 (MWM/ZSM); 2, *Eugoa* Walker, [1858], slide AV3109 (CAV); 3, *Collita* Moore, 1878, slide ZSM Arct. 2019-1098 (MWM/ZSM); 4, *Lophilema* Aurivillius, 1910, slide BMNH Arct. 5622 (©The Trustees of NHMUK); 5, *idem*, slide AV3188 (ANHRT).



Figures 6–10. Details of the male genitalia structures of Lithosiini. 6, *Siccia* Walker, 1854, slide AV7119 (OUMNH); 7, *Spatulosia* Toulgoët, 1965, slide AV5626 (ANHRT); 8, *Teulisna* Walker, 1862, slide ZSM Arct. 2021-363 (MWM/ZSM); 9, *idem*, slide AV7113 (OUMNH); 10, *Pseudopoliosia* Krüger, 2015, slide AV6848 (ANHRT).

Valva

The Lepidoptera gonopods are termed ***valvae*** (Burmeister 1832) (=*harpago* of White (1876)). Each valva is a hollow lobe attached to the posterior margin of the vinculum and directed caudally. Birket-Smith (1965) termed the whole ventral part of the valva as 'ala valvae' and the dorsal portion as the 'supravalva'. However, these terms have limited applicability, and only to those Lithosiini with clearly subdivided valva (mostly of the subtribe Lithosiina), thus cannot be accepted for the tribe as a whole.

The basic sclerite of the valva can be conditionally subdivided into three parts. The basal one is a carcass of the anterior (proximal) margin of the valva articulated with the caudal margin of the vinculum, and can be termed as the ***basis valvae*** (Birket-Smith 1965). The sclerotised extensions of its dorsal and ventral regions are called the ***costa*** (Pierce 1914) and ***sacculus*** (Pierce 1909), respectively. In some genera the basis valvae bears a crest-like thickening, termed the ***jugum basalis*** (nom. nov.) (Fig. 10) which creates the illusion of a suture between the basis valvae and the sacculus, which may be the reason why Birket-Smith (1965) considered the sacculus as an independent sclerite. In certain groups, besides the *jugum basalis*, the outer wall of the valva bears additional crest-like thickenings, which are extensions of the basis valvae and probably serve as additional stiffening ribs. There are two main types of such structures: the longitudinal branch of the *jugum basalis*, the ***jugum distalis*** (nom. nov.) (Fig. 10), and the transversal ***arcus*** (nom. nov.), which is more or less arcuate, stretching from the ventral margin of the sacculus to the costa (Fig. 11).

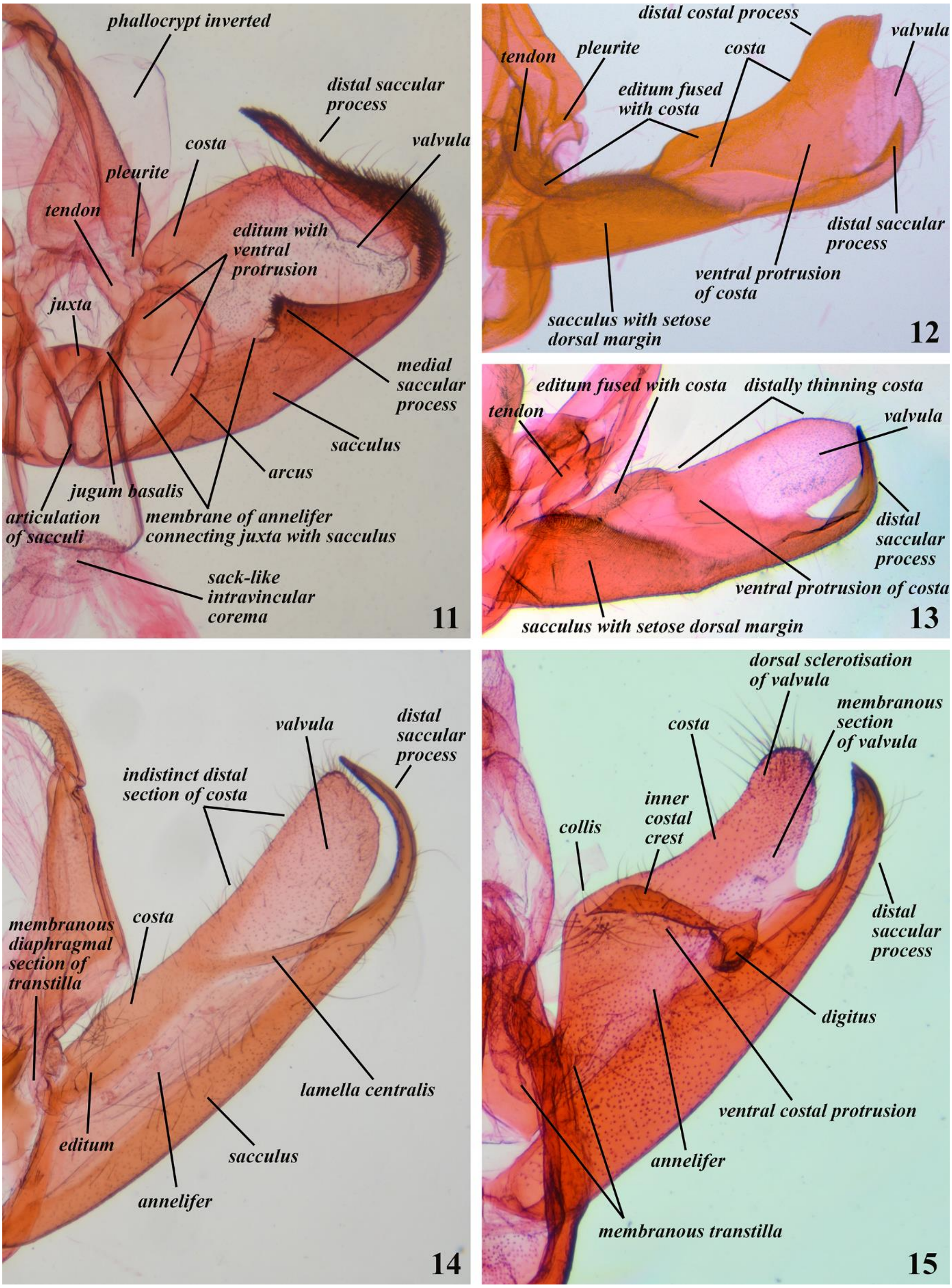
In many groups of Lithosiini the ***costa*** forms an outer carcass of the dorsal section of the valva, occupying the main part of the dorsal margin of the valva and its distal section can be extended into a free process (the ***distal costal process***) (Fig. 12) or gradually thin distally and not protrude towards the dorsal margin of the valva (Fig. 13). In rarer cases, the distal end of the costa is indistinct due to the gradually weakening sclerotisation, which becomes distally indistinguishable from the secondary sclerotisation of the valvula (Fig. 14).

In the groups in which the costa forms the dorsal margin of the valva, the latter can have a medial protrusion, the ***collis*** (nom. nov.) (Figs 1, 15). Besides the distal process, the costa can bear a process (smooth or setose) on the inner surface of its main (dorsal) part, the ***digitus*** (Fig. 15). This term is widely accepted for homologous processes in Noctuidae and therefore is used preferentially in the present paper. Additionally, in certain genera (e.g., *Cyana* Walker, 1854) the ventral protrusion of the costa can bear an ***inner costal crest*** stretching from the collis to its ventral end (similar to the crest of the lamella centralis), which can be present together with the digitus (Fig. 15), and sometimes fused with it.

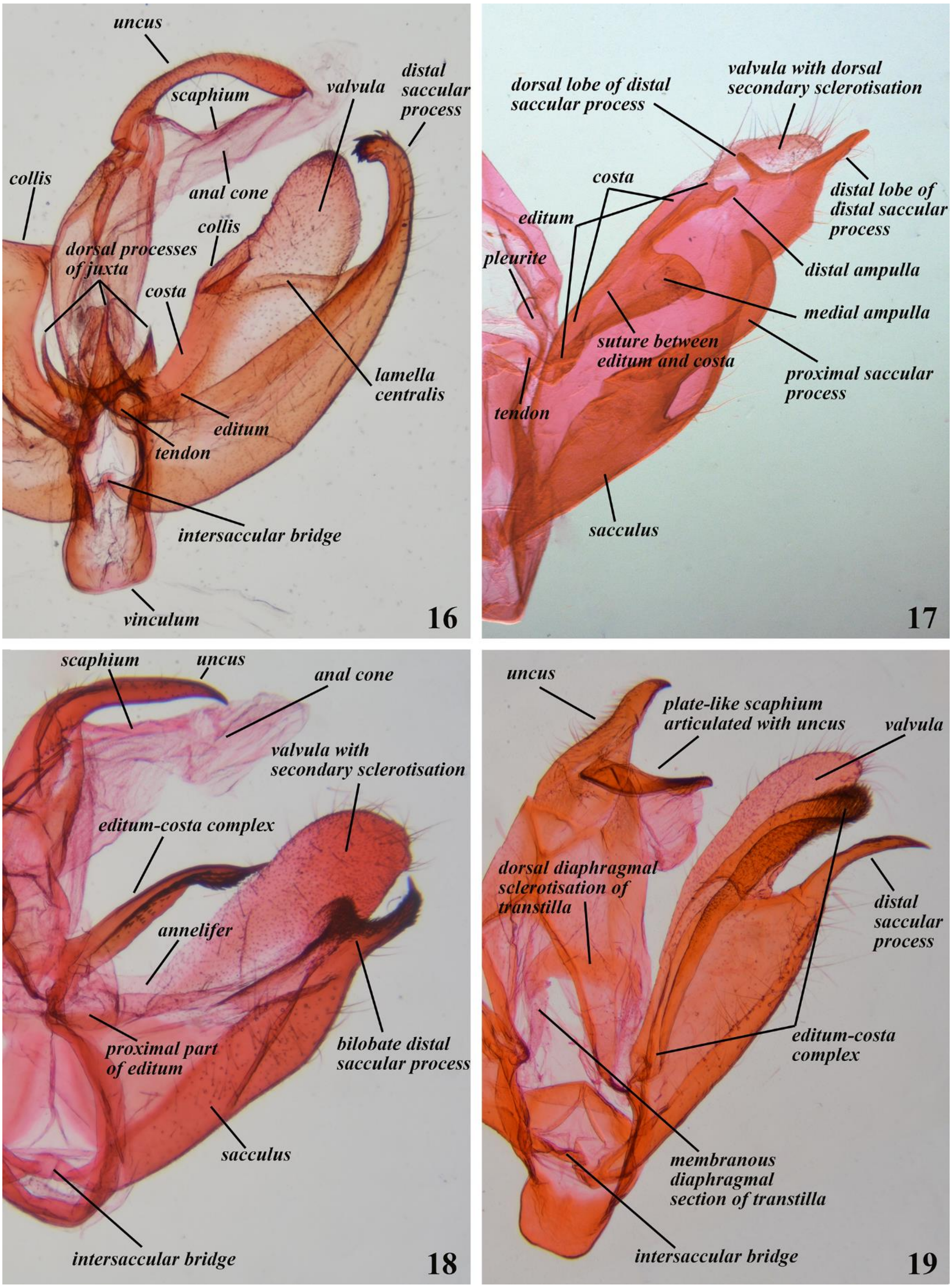
The inner surface of the valva bears a fold stretching along the ventral margin of the costa and continued mesad into the diaphragm, stretching dorsad of the anellus, which is termed the ***transtilla***. The transtilla is membranous in certain groups (Fig. 15) but in a number of Lithosiini the valval part of the transtilla is sclerotised forming an elongate sclerite, which is herein suggested as being termed the ***editum*** (Figs 2, 3, 10, 11, 14). In Lithosiini the editum can be free (Fig. 10) or fused with the ventral margin of the costa (Figs 12, 13), but in most groups these sclerites are firmly articulated proximally or longitudinally, and the suture is recognisable (Figs 16, 17). In certain genera the editum is displaced dorsad and serves as a proximal part of the carcass of the dorsal margin of the valva while the proximal part of the costa lies on the outer wall of the valva wrapping into the inner wall only medially (Figs 12, 13). In extreme cases, the editum and the costa are fully fused and form an ***editum-costa complex***, which can be: (1) separated from the medial region of the valva and erected dorsad as a heavily sclerotised process (Fig. 18); (2) stretched along the dorsal margin of the valva with only its distal end separated as a process (Fig. 19); and (3) solely forming the dorsal section of the valva while the valvula is reduced (Fig. 20).

The surface of the editum can be setose (Fig. 13), smooth (e.g., Figs 10, 11), or bear clusters of spinules (Fig. 21). The editum can have a process originating from its distal or medial section or from its ventral protrusion, the ***ampulla*** (Figs 17, 26). In some taxa two ampullae co-exist and it is suggested they are referred to thus: e.g., ***medial*** and ***distal ampulla*** (Fig. 17). In certain Lithosiini genera the ampulla is lobular and directed more or less ventrad (Fig. 17), which has been incorrectly referred to in the past as the 'digitus' (Witt *et al.* 2011), 'central process of costa' (Holloway 2001), or 'medial costal process/extension' (e.g., Volynkin & Černý 2016, 2017a).

Besides the processes originating from the inner surface and the dorsal and ventral margins of the valva, there are also ental processes, i.e. the processes directed mesad (into the annulus). In



Figures 11–15. Details of the male genitalia structures of Lithosiini. 11, *Nyea* Agenjo, 1983, slide AV8567 (ANHRT); 12, *Miltochrista*, slide AV2291 (CAV); 13, *idem*, slide MWM 31.512 (MWM/ZSM); 14, *Pseudotigrioides* Krüger, 2015, slide ZSM Arct. 2021-126 (MWM/ZSM); 15, *Cyana*, slide AV5113 (ANHRT).



Figures 16–19. Details of the male genitalia structures of Lithosiini. 16, *Birketsmithiola* Krüger, 2015, slide AV6786 (ANHRT); 17, *Barsine* Walker, 1854, slide AV1765 (CAV); 18, *Bechuanosia* Krüger, 2015, slide AV7266 (ANHRT); 19, *Tesma* Birket-Smith, 1965, slide AV6354 (ANHRT).

Lithosiini, ental processes of two kinds are recognised: the ***processus momenti*** (Birket-Smith 1965) arising from the costa (or the dorsal corner of the basis valvae) (Figs 26, 28), and the ***tendon***, which is a sclerotisation of the diaphragmal part of the transtilla extending mesad from the editum (Figs 3, 10–13, 16, 17, 21). In certain groups, the processus momenti and tendon co-exist and can be free (Fig. 28) or fused with each other, forming a plate with well-sclerotised dorsal and ventral sections corresponding to the processus momenti and the tendon, respectively, and a more weakly sclerotised inner area sometimes having window-like membranous areas. This complex structure is herein suggested to be termed the ***conjuga*** (nom. nov.) (Fig. 22).

In the central part of the inner surface of the valva, sclerotised plates of three different origins can be present. Two of them are ventral protrusions of the costa and the editum, and it is suggested herein that they are referred to as the ***ventral protrusion of costa*** (Figs 1, 7, 12, 13, 15) and the ***ventral protrusion of editum*** (Fig. 11). Besides these structures, another elongate transverse sclerotised plate is found in the middle region of the valva of a number of Lithosiina genera. It was impossible to find a term applicable to this structure in the literature devoted to Noctuoidea morphology and taxonomy, and therefore a new term is introduced for it, the ***lamella centralis*** (nom. nov.). This sclerite can be free (Fig. 10) but in many cases it is ventrally articulated or fused with the dorsal corner of the base of the distal saccular process, and can be extended dorsally up to the ventral edge of the costa (Fig. 14) or editum (Fig. 16), sometimes firmly articulated or fused with them. In the latter case it can be difficult to separate the lamella centralis from the ventral protrusion of the editum or costa. The lamella centralis can be fold-like (Fig. 10) or flat (Figs 14, 25), and, additionally, may be smooth (Fig. 14) or bear a cluster of setae (Figs 10, 25); in a number of groups it also bears a longitudinal crest-like process, which can be descriptively called the ***crest of lamella centralis*** (= ‘harpe’ *sensu* Dubatolov & Zolotuhin (2011)) (Fig. 23).

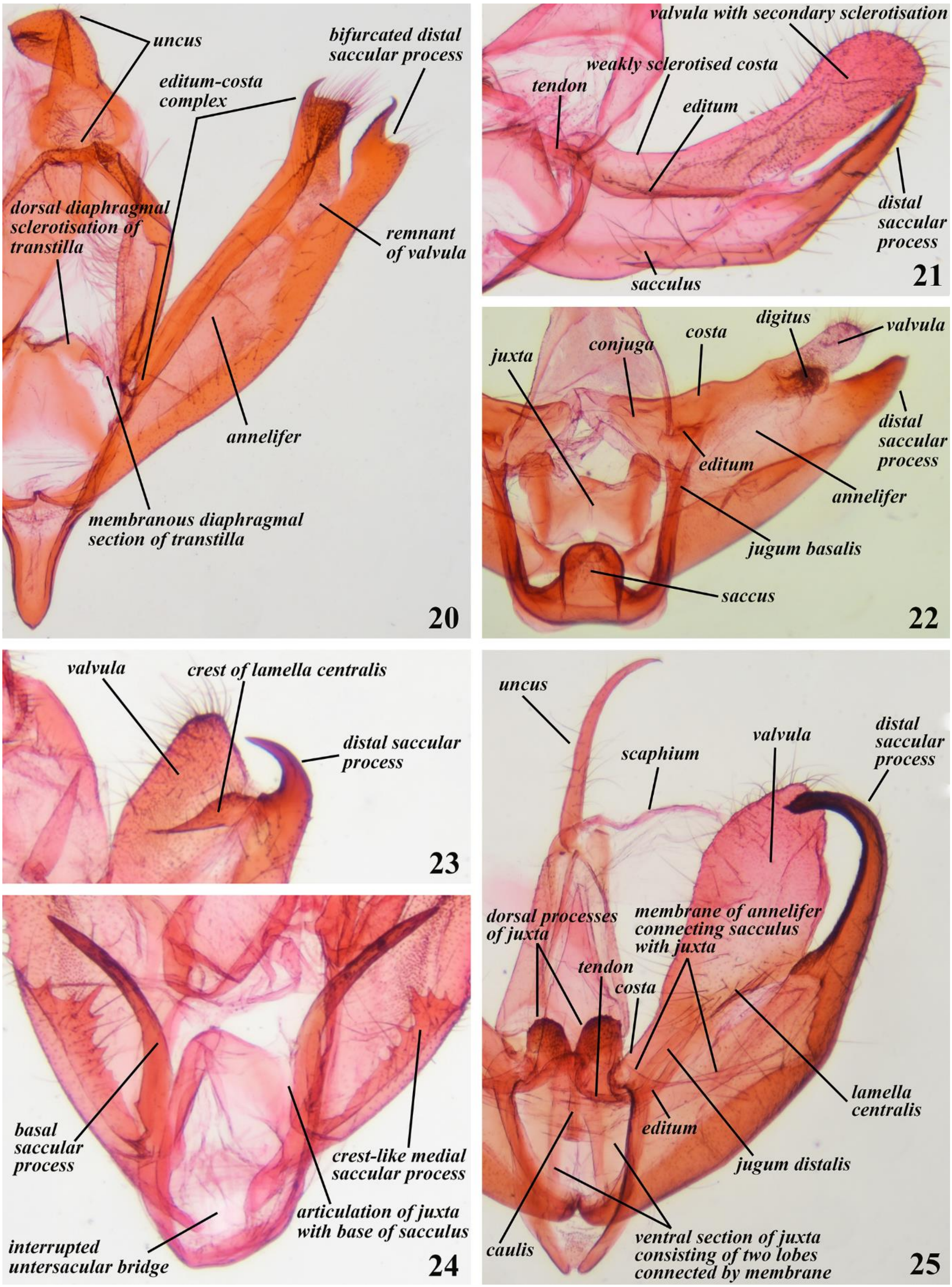
The aforementioned term ***valvula*** refers to the weakly sclerotised, often membranous and setose ventro-distal region of the valva, which is sometimes separated as a lobe. In some groups of Lithosiini the valvula is vestigial (Fig. 20) or reduced to a membranous region not protruding beyond the margin of the valva (Figs 2, 7). Valvula can bear a cluster of heavily sclerotised and barely detachable setae (Figs 1, 7), which is herein suggested to be termed the ***iuba*** (nom. nov.), the structure reminiscent of but not homologous to the corona in the Noctuidae.

The proximal membranous area of the inner surface of the valva between the costa/transtilla region and the dorsal margin of the sacculus is called the ***annelifer*** (Sibatani *et al.* 1954) (e.g., Figs 14, 1, 20, 22). In Lithosiini it can be very short and narrow or occupy a significant part of the inner proximal surface of the valva, only distally restricted by one of the transverse sclerotised formations; in the genera with a separated editum-costa complex the annelifer forms the dorsal margin of the valva (Fig. 18). The proximal region of the annelifer is fused with the lateral wall of the anellus but in certain genera the membrane of the annelifer is enlarged and forms a fold connecting the inner surface of the valva with the juxta (Figs 11, 25).

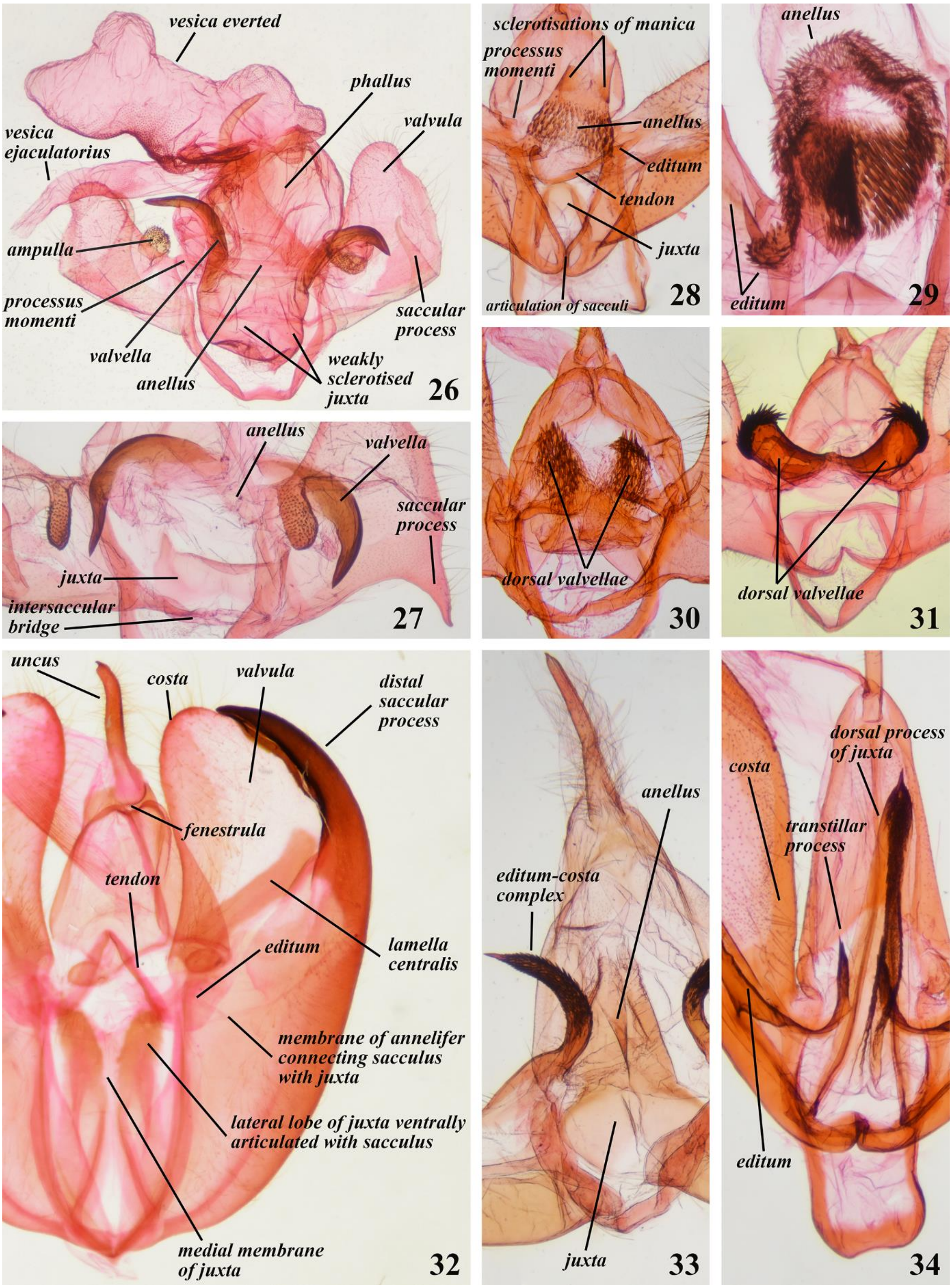
The ventral-distal enlargement of the basis valvae is the ***sacculus*** (e.g., Figs 1, 2, 10–14, 17, 18, 21). It forms the carcass of the ventral part of the valva and in most groups its proximal section is relatively broad due to the sclerotisation extended dorsad, and contains the majority of the intravalval muscle. The proximal end of the muscle is attached to either the basis valvae or the ventral margin of the sacculus. In certain groups the sacculus bears processes, which can be descriptively called: ***proximal*** (or, alternatively, ***basal***), ***medial*** or ***distal saccular processes***. The last is present in most genera of Lithosiini and is usually unilobate. However, in certain species-groups and genera it may be bifurcate (Fig. 20) or bear an additional ventral lobe situated more proximally (Fig. 17). Besides the processes, the dorsal margin of the inner surface of the sacculus can bear a cluster of setae or denticles.

The sacculi can be free and separated from each other by the ***intravincular membrane*** (Figs 1, 2, 7, 33) but more frequently they are ventrally firmly articulated (e.g., Figs 11, 28) or the ventral ends of the bases valvae are extended mesad and fused with each other forming the sclerotised ribbon-like ***intersaccular bridge*** (nom. nov.) (Figs 3, 10, 16, 18, 19, 20, 25, 30, 31), which was assumed by Kristensen (2003a) to be a groundplan trait within Lepidoptera. The intersaccular bridge can be interrupted by the intravincular membrane in some genera (Fig. 24).

In certain groups the sacculus can be connected to the distal section of the juxta via a thin membrane representing an enlargement of the annelifer, which is attached to the whole dorsal margin of the sacculus or its proximal part (Fig. 11). Additionally, in some genera the proximal margin of the



Figures 20–25. Details of the male genitalia structures of Lithosiini. 20, *Dubatoloviana* Bucsek, 2012, slide ZSM Arct. 2021-095 (MWM/ZSM); 21, *Pusiola* Wallengren, 1863, slide AV7141 (ANHRT); 22, *Cyana*, slide AV4984 (ANHRT); 23, *Tarika* Moore, 1878, slide ZSM Arct. 2021-268 (MWM/ZSM); 24, *Architosia* Birket-Smith, 1965, slide AV7138 (ANHRT); 25, *Wittia* de Freina, 1980, slide AV8568 (ANHRT).



Figures 26–34. Details of the male genitalia structures of Lithosiini. 26, *Cragia* Birket-Smith, 1965, slide AV8569 (ANHRT); 27, *idem*, phallus removed, slide AV8572 (ANHRT); 28, *Teulisna*, slide ZSM Arct. 2021-115 (MWM/ZSM); 29, *Palaeugoa*, slide AV8535 (ANHRT); 30, *Campteropsis* Krüger, 2016, slide AV6438 (ANHRT); 31, *Lobilema* Aurivillius, 1910, slide AV3194 (ANHRT); 32, *Chrysorabdia* Butler, 1877, slide ZSM Arct. 2021-219 (MWM/ZSM); 33, *Arctiananna* De Prins, 2021, slide AV6964 (ANHRT); 34, *Oedipygilema* Krüger, 2015, slide AV6476 (ANHRT).

sacculus is firmly articulated with the juxta (with the lateral or proximal parts of its lateral margins) (e.g., Fig. 24). Moreover, in some genera the ventral margins of the sacculi or their proximal parts can be connected to each other via a thick-walled membrane termed the ***commissure*** (Dubatolov *et al.* 2021). In extreme cases (e.g., in the genus *Chinasa* Dubatolov, Volynkin & Kishida, 2018) the dorsal margins of the valvae are fully fused, which makes the male clasping apparatus capsule-like with only the distal saccular processes and the valvulae remaining free.

Diaphragm, periphallic region and phallus

The membranous ventral body wall inside the annulus between and dorsally from the valvae is called the ***diaphragm*** and in the middle of it is situated the *phallobase*. In Noctuoidea the latter represents an invagination of the body wall forming a membranous pocket, the ***phallocrypt*** (Snodgrass 1935). From the bottom of the phallocrypt the intromittent organ called the ***phallus*** originates. The latter is often called *aedeagus* in numerous works devoted to various groups of Lepidoptera but Kristensen (2003a) suggested replacing this term with the more neutral term phallus as the sclerotised tube these terms refer to is homologous with the phallotheca rather than the true aedeagus.

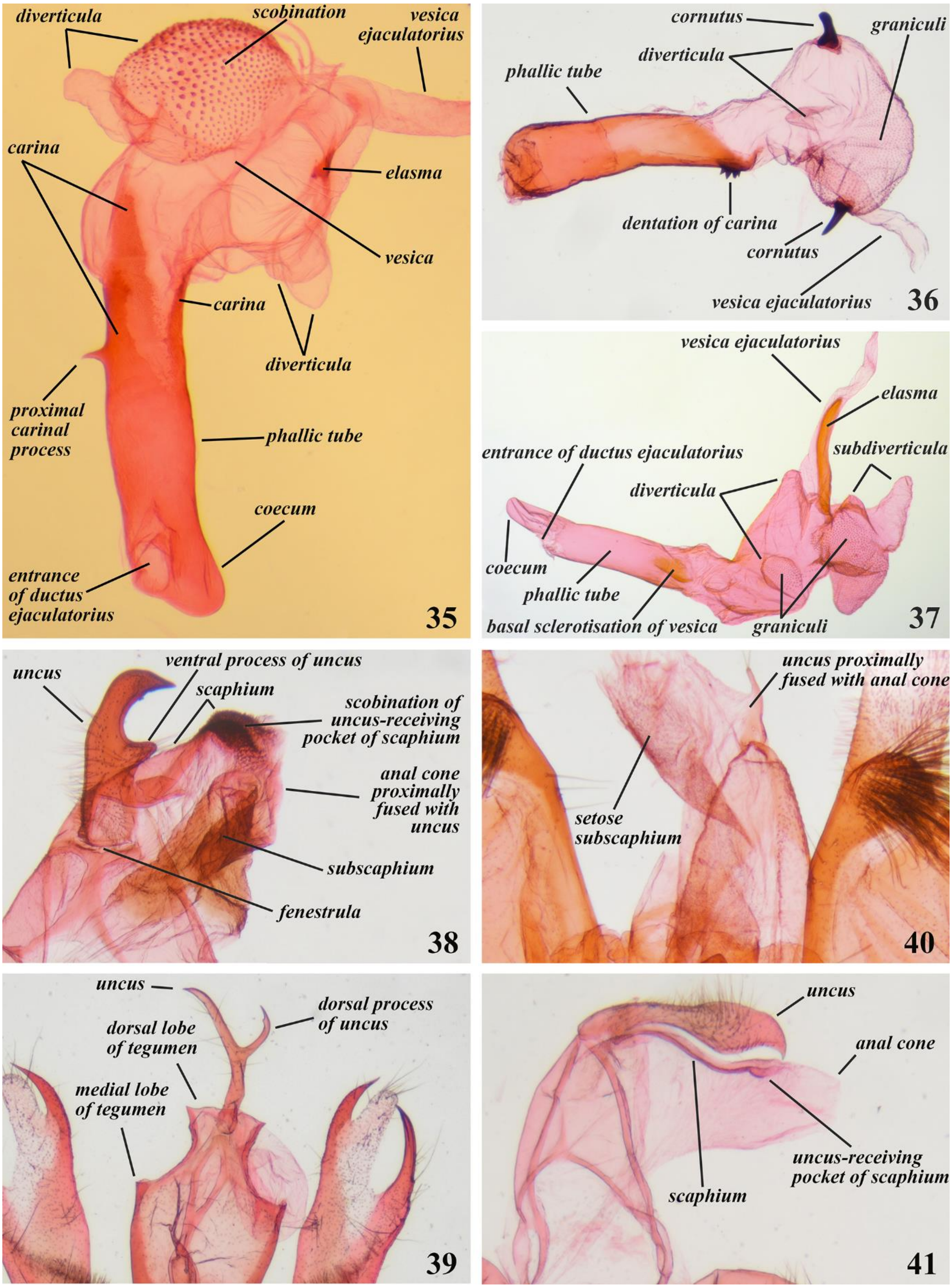
The periphallic region of the diaphragm has several structures bearing sclerotisations. The collar-like fold surrounding the phallocrypt entrance is the ***anellus*** (Busck & Heinrich 1921) and in a number of groups it bears various sclerotisations such as clusters of graniculi or spinules (Figs 28, 29), and sclerotised plates. In a few Lithosiina genera the anellus bears a pair of heavily sclerotised process- or lobe-like structures called ***valvellae*** (Birket-Smith 1965, partim.) (Figs 26, 27, 30, 31). The valvellae are in most cases situated laterad or dorso-laterad of the phallus, and often fused with the anellus and form an integrative part of the intromittent complex (Birket-Smith 1965). The phallocrypt itself can also bear some sclerotisations in its posterior region called the ***manica*** (Fig. 28).

The ventral sclerotised formation supporting the phallus is termed the ***juxta***. It is assumed to be homologous to the 'median plate' ('*lamella medialis*') (Kuznetzov & Stekolnikov 2001; Kristensen 2003a) and can be a solid plate (e.g., Figs 1, 6, 7, 21, 27) or consist of two ***lateral lobes*** medially connected via a ***medial membrane*** (Fig. 32), but in most groups these plates are partly (distally/dorsally) fused and the juxta has ventral membranous regions of various shapes (e.g., Figs 3, 11, 20, 22, 24, 25, 28, 31, 34). The juxta shape is generically very diverse and it can additionally bear one or a few processes apically (dorsally) (Figs 3, 16, 22, 25) or on its ventral surface. In certain genera the distal (dorsal) region of the juxta is extremely enlarged and produced into a process of various shapes (Fig. 34). The distal region of the juxta can be connected to the anellus via a sclerotised band- or rod-like plate called the ***caulis*** (Kristensen 2003a) (Fig. 25). In extreme cases the juxta can be fused with the ventral wall of the anellus (Fig. 33).

Besides the aforementioned sclerotisations, the diaphragm can bear free ***transtillar processes***, which are often dorsal extensions of the tendon (Fig. 34) but in certain genera they are located on the membranous transtilla, for example, in the genus *Palaeugoa* Durante 2012, in which the lobe-like transtillar processes were erroneously called paratergal sclerites (Durante 2012).

The ***phallus*** of Lithosiini is more or less cylindrical, sometimes distally dilated or up- or downcurved, and in most cases its anterior end has a closed protrusion called the ***coecum*** (Figs 35, 37), which performs the function of an apodeme for attachment of *the protractor of phallus* (Forbes 1939) numbered by Birket-Smith (1965) as 'm. 6'. Kuznetzov & Stekolnikov (2001) called this muscle *musculus phallicus externus posterior* and numbered it as 'm_5'. The phallic tube surrounds the membranous *endotheca* (Kristensen 2003a), which is eversible and called the ***vesica*** (Figs 35–37). The distal end of the phallic tube can bear sclerotised crests or weakly sclerotised band-like protrusions extending into the basal section of the vesica (Figs 35, 36). In this case those structures are invaginated into the phallic tube together with the vesica and Birket-Smith (1965) introduced the term 'pseudoaedeagus' in reference to them. However, following the concept widely accepted in Noctuoidea taxonomic publications, it is suggested herein to use the term ***carina*** for any kind of distal phallic extensions (Kononenko 2010). In certain groups, the carina may bear dentations (Fig. 36) or one or a few free processes (***carinal processes***) directed distally or sideways (Fig. 35).

When everted, the vesica can be significantly longer and broader than the phallic tube. Vesicae of different genera are very diverse in configuration and can have ***diverticula*** (sing.: *diverticulum*) of various shapes (Figs 35–37), which may have additional ***subdiverticula*** (Fig. 37), and/or bear clusters/fields of ***graniculi*** or ***spinulose scobination*** (Figs 35–37), or heavily sclerotised ***spines*** or



Figures 35–41. Details of the male genitalia structures of Lithosiini. 35, *Vamuna* Moore, 1878 *s.l.*, slide ZSM Arct. 2019-957 (MWM/ZSM); 36, *Pseudotigrioides*, slide ZSM Arct. 2021-126 (MWM/ZSM); 37, *Padenia* Moore, 1882, slide AV1707 (CAV); 38, *Kruegerilema* Volynkin & László, 2021, slide AV8575 (ANHRT); 39, *Miltochrista*, ZSM Arct. 2019-1016 (MWM/ZSM); 40, *Cyana*, slide AV6335 (ANHRT); 41, *Siccia*, slide AV6871 (ANHRT).

cornuti (sing.: *cornutus*) (Fig. 36). The latter are diverse in size and shape and can have a strongly dilated base which, in the case of a reduction of the protruding part, can be transformed into a sclerotised plate.

The terminal duct of the vesica bearing a functional gonopore is the ***vesica ejaculatorius*** (Fibiger 1997) (Figs 35–37) and in certain groups, another kind of sclerotised plate is found at its base (Holloway 2001), which may be referred to as the ***elasma*** (nom. nov.) (Figs 35, 37) (also often called in literature 'the basal plate of vesica ejaculatorius' or 'distal plate of vesica'). This sclerite is not unique to the Lithosiini and also found in some other groups of Erebidae as well as Euteliidae (Holloway 1985, 2005; Kitching & Rawlins 1998; Goater *et al.* 2003). The function of this structure is unclear but it is assumed herein to be an insertion point for the intraphallic muscle functioning as the retractor of the vesica; nevertheless, the intraphallic musculature of various groups of Lithosiini remains largely unknown and requires further extensive studies. The aforementioned vesica ejaculatorius can originate from various regions of the vesica body and its distal section is situated outside the phallic tube in the membranous duct which is a posterior section of the ***ductus ejaculatorius*** (Klots 1970; Kristensen 2003a, 2003b). The entrance of the latter in most cases opens in the posterior part of the dorsal wall of the phallic tube, or, more rarely (Figs 35–37), if a coecum is not developed, in the anterior end of the phallus or even somewhat ventrally.

The 10th segment

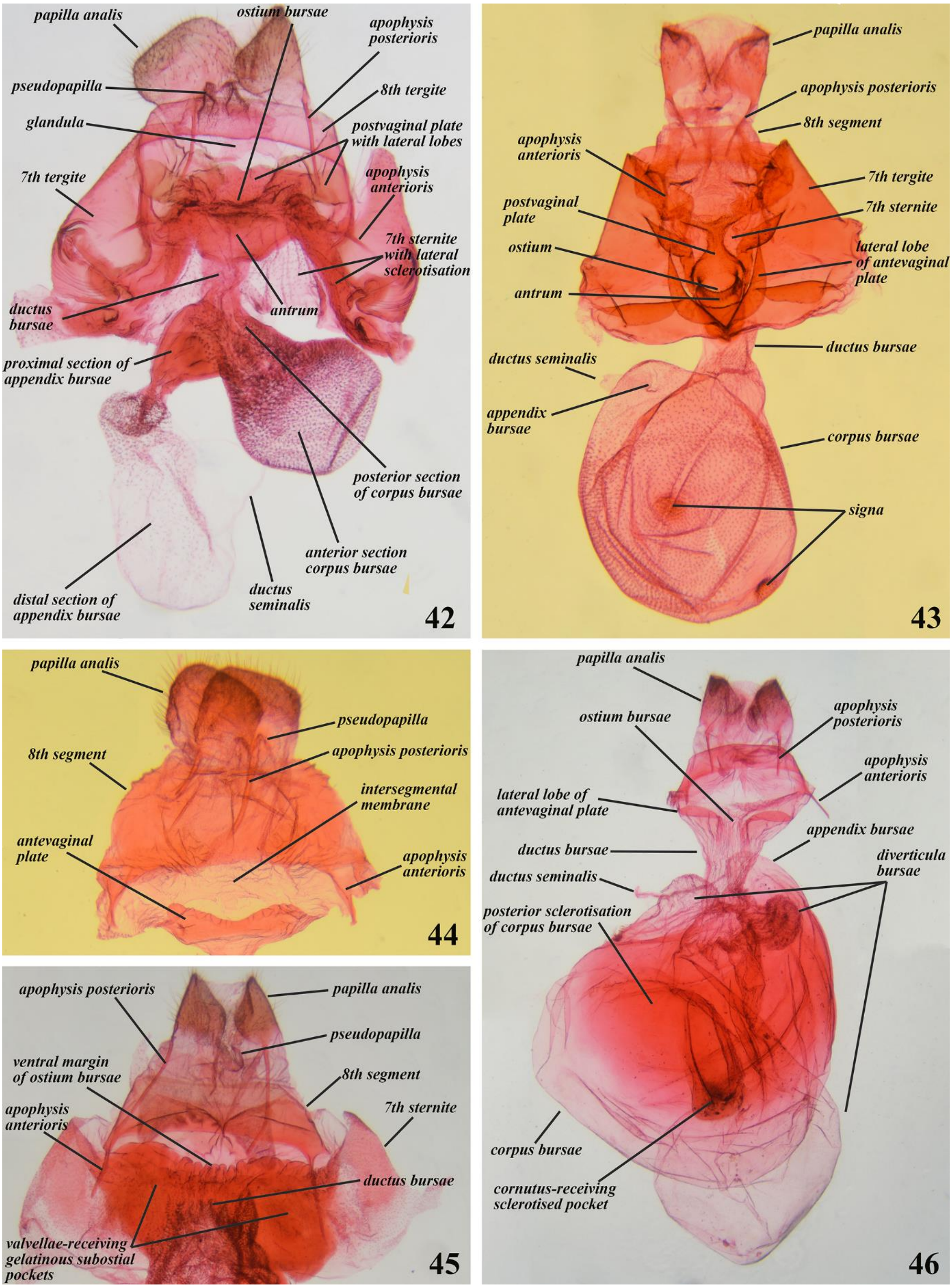
The derivative of the 10th abdominal tergum is termed the ***uncus***. In Lithosiini it is usually hook- or plate-shaped, dorso-ventrally or laterally flattened, more rarely swollen (e.g., Figs 2, 16, 18–20, 25, 32, 41), distally bilobate or bearing a process dorsally, ventrally or laterally (Figs 2, 38, 39). The uncus can be smooth or bear a cluster of setae and at its base is plate-like in many groups. A membranous area between the tegumen and uncus is called the ***fenestrula*** (Kristensen 2003a) (Figs 32, 38). Ventrad of the uncus, the membranous ***anal cone*** (=*tuba analis*) is situated, on the apex of which the anus is located. In many genera of Lithosiini the anal cone bears sclerotisations: the dorsal one is called the ***scaphium*** (e.g., Figs 16, 18, 19, 25, 38, 41) while the ventral one is termed the ***subscaphium*** (Figs 38, 40). In certain groups the uncus is weakly sclerotised and partly or even fully fused with the dorsal wall of the anal cone (Fig. 40). The scaphium is usually rod- or string-like (more rarely, plate-like), sometimes heavily sclerotised, and proximally connected to the base of the uncus (Figs 16, 19, 38, 40). In certain genera the scaphium is plate-like, heavily sclerotised and is larger than the uncus. In species with a downcurved and apically pointed uncus the scaphium bears a distal pocket, which receives the tip of the uncus in resting position (Figs 38, 41). This structure is already observed in other groups of Erebidae (Lödl 2000; Holloway 2005) and Noctuidae (Figs 51, 52). The subscaphium is in most cases a weakly sclerotised plate or a cluster of tiny setae or fine scobination (Fig. 40), but in extreme cases it can be enlarged and heavily sclerotised (Fig. 38). The subscaphium is assumed to be a derivative of the 10th sternum (Kuznetzov & Stekolnikov 2001) while no specific information about the origin of the scaphium was found; it is possible that the scaphium, as well as the uncus, is a derivative of the 10th tergum. Both these sclerotisations serve as insertion points for 'muscle no 2' (Birket-Smith 1965) from the dorsal part of the tegumen referred to as *the retractor of anal tube* by Forbes (1939), which is inserted at the base of the anal cone if the latter lacks both the scaphium and subscaphium.

Female genitalia

The present section focuses on the 7th–10th abdominal segments and the cuticle-lined inner compartments of the female genitalia such as the bursa copulatrix and ductus seminalis, which are used for diagnostic purposes, while other membranous reproductive structures (described in detail by Kristensen (2003a, 2003b)) are not dealt with.

The 8th–10th abdominal segments of female Lithosiini form an ovipositor. The 9th and 10th segments form the abdominal apex, which bears the ***papillae anales***, a pair of lateral lobes, which are setose and in most Lithosiini weakly sclerotised. Papillae anales enclose the membranous area where the *ovipore* and the *anal orifice* are situated. In certain genera, on the ventral side of the ovipositor, between the papillae anales there is a pair of finger-like or fold-like setose structures, the ***pseudopapillae*** (Bendib & Minet 1999) (Figs 42, 44, 45). This structure is also known in the Erebidae subfamily

Lymantriinae (Holloway 1999), for which the term was originally introduced (Maes 1984). A similar structure is also known in the Noctuidae subtribe Apameini (Noctuinae) but it is currently impossible to state whether they are homologous.



Figures 42–46. Details of the female genitalia structures of Lithosiini (all in ANHRT). 42, *Palaeugoa s.l.*, slide AV8532; 43, *Siccasura* Volynkin & László, 2021, slide AV6122; 44, *Palaeugoa*, slide AV5984; 45, *Cragia*, slide AV7282; 46, *Crocosia* Hampson, 1914, slide AV8576.

In a number of groups of Lithosiini as well as Arctiini and Syntomini, the intersegmental membrane between the papillae anales and the 8th abdominal segment dorsally bears a sack-like pheromone gland, which is considered an autapomorphy of the subfamily Arctiinae (Holloway 1988; Bendib & Minet 1998) (Fig. 42). The size and shape of this gland varies greatly in different groups, and it can also be secondarily absent (e.g., in the Madagascan *Phryganopteryx* Saalmüller, 1884) (Bendib & Minet 1998, 1999). However, despite the structural diversity, the shape of this female pheromone gland was found to be slightly variable individually in Afrotropical *Cyana* (Karisch 2013) and thus difficult to utilise for purposes of alpha-taxonomy. In the latter paper, the dorsal pheromone gland was called the ***glandula*** and this term is accepted herein to refer to this particular structure of Lithosiini for reasons of convenience.

The 8th abdominal sternite of Lithosiini is narrow and in most groups membranous while the lateral parts of the 8th abdominal tergite are enlarged and extend ventrad forming the lateral and partly ventral sclerotised wall of the segment. In rarer cases, both the 8th sternite and tergite are sclerotised and fully fused forming a cone-like formation (Fig. 44). The anterior margins of the papillae anales and the 8th sternite laterally bear paired apophyses, the ***apophyses posteriores*** and ***apophyses anteriores***, respectively, which are apodemes of the group of apophysal muscles (*musculi apophisales*) (Kuznetzov & Stekolnikov 2001) and are situated inside the body. The apophyses are usually rod-like but may have dilated and flattened anterior and/or posterior ends (Figs 42–46).

The copulatory orifice is termed the ***ostium bursae***, which is situated on the ventral side of the abdomen and its position is varied within the tribe Lithosiini. In most groups, the ostium bursae is situated between the 7th and 8th sternites and is articulated with the 8th sternite. The ventral margin of the ostium bursae can be attached to the 7th sternite via a membrane or fused with its posterior margin (Figs 42, 45). In this instance, the 7th sternite may bear various subostial and lateral sclerotisations including the ***lateral plates*** which bear a ***corethrogyne*** or lateral, usually ***gelatinous pockets*** serving for insertion of the distal saccular processes during copulation. The subostial area of the 7th sternite can also bear lateral (more rarely ventral) sclerotised or gelatinous pockets serving as an attachment for the carinal processes, valvellae (Fig. 45), or processes of the juxta during copulation. In certain genera the 7th sternite is modified and heavily sclerotised or the whole 7th segment is sclerotised and transformed into a capsule-like structure bearing various sculptures (Fig. 43). In some groups the ostium bursae is displaced deeper into the 7th sternite, where it is located on the 'bottom' of the medial concavity of the posterior margin of the sternite, while in other groups, it opens in the middle of the sternite (Fig. 43).

The region posteriorly of the ostium bursae is called the ***postvaginal area***, and in different groups it belongs to the 7th poststernum or the intersegmental membrane. The sclerotised formation surrounding the ostium bursae is termed the ***sterigma***, which can be solid or more frequently, is represented by one of the two sclerites, the ***postvaginal plate*** in the postvaginal area (Figs 42, 43) or the ***antevaginal plate*** (Fig. 44) located anteriorly from the ostium bursae. In some groups both the plates are present while in others, the sterigma is absent and the subostial area is membranous. The antevaginal plate can be subdivided into two lateral lobes (Fig. 43), which are independent of each other (Fig. 46).

The ostium bursae opens into the *bursa copulatrix*, which is a ventral appendix of the *genital chamber* serving as a depository for *spermatophores* (Kristensen 2003a, 2003b). In Lithosiini it is subdivided into an anterior dilated part, the ***corpus bursae*** (Figs 42, 43, 46), and a narrower duct-shaped posterior section leading to the ostium bursae called the ***ductus bursae*** (Figs 42, 43, 46). The bursa copulatrix is connected to the dorsal part of the genital chamber via the ***ductus seminalis***, which arises from the ***appendix bursae*** (= '*apex bursae*' *sensu* Ronkay 1986) or, rarely, from the wall of the corpus bursae. In cases of the corpus bursae gradually narrowing posteriorly making the border between it and the ductus bursae unclear, it is suggested herein to use the source of the ductus seminalis for delimitation. The ductus seminalis can be dilated very near the appendix bursae forming the ***bulla seminalis***, which has various functions in different groups (Kristensen 2003b): pumping the sperm from the bursa copulatrix to the genital chamber (Norris 1932), serving as sperm storage (LaMunyon 2000), or crushing the unfertilised eggs for oosorption (Lum 1979, 1984).

The ductus bursae is diverse in its shape, size and sclerotisations in various groups of Lithosiini. In many genera it is posteriorly dilated and forms the ***antrum***, which in most cases has sclerotised or gelatinous walls or, rarely, is funnel-like and membranous (Fig. 46). In certain groups, the antrum bears sclerotised plates or ventral longitudinal folds making it expandable. The ductus bursae itself can be tubular or dorso-ventrally flattened, with membranous or gelatinous walls frequently bearing sclerotised plates or longitudinal wrinkles.

The corpus bursae is more or less sack-shaped in most groups of Lithosiini. In certain genera it is subdivided into the ***anterior*** and ***posterior sections*** (Fig. 42), of which the latter is usually broader and has more weakly sclerotised (often membranous) walls (Fig. 46), but in many groups also bears sclerotised plates called ***signa*** (sing.: *signum*) (Fig. 43). The number of signa and their shape are very diverse within the tribe. The posterior section of the corpus bursae can be entirely gelatinous and/or bear gelatinous protrusions or pockets, areas of diffuse sclerotisation, sclerotised plates or clusters of spines. All these structures as well as signa serve as attachment points for the corresponding sclerotisations of the male vesica during copulation, as demonstrated and discussed by Mikkola (2008) in the Noctuidae. Klots (1970) used the term *cervix bursae* (=*praebursa*) for the "differentiated region between ductus bursae and corpus bursae, often with special sclerotizations or invaginations of its wall" which may refer to the posterior section of the corpus bursae when it is modified and ornamented. Since this region of the bursa copulatrix in Lithosiini is often very large and occupies about a half or more of the corpus bursae, the use of the term 'cervix bursae' meaning 'neck of bursa' should be avoided. Besides the signa and sclerotised plates, sclerotisations such as ***clusters of spines*** or ***spinulose scobination*** occur in the corpus bursae of a number of genera (Figs 42, 43), and in certain groups a whole corpus bursae or for the most part is densely covered with spinules.

It is suggested herein to use the term appendix bursae to refer to the lobe of the corpus bursae, from which the ductus seminalis arises (Figs 42, 43, 46), while other closed extensions of the corpus bursae can be termed as the ***diverticula bursae*** (nom. nov.) (sing.: ***diverticulum bursae***) (Fig. 46). It is also worth mentioning that the aforementioned term *cervix bursae* is sometimes used in Noctuoidea taxonomy as synonymous to the structure called herein as the appendix bursae (e.g., Varga 1990; Mikkola 2008), and this confusion is another reason for not applying this term. The location of the appendix bursae and its shape, size and structure are very diverse in Lithosiini and in most cases it is situated postero-laterally, or, more rarely postero-ventrally, medio-laterally or anteriorly. The appendix bursae usually has a broad base and is gradually tapered distally but in certain groups it has a narrower and gelatinous or sclerotised ***proximal section*** while its distal part is strongly dilated and membranous (Fig. 42). In most groups of Lithosiini, the corpus bursae is significantly larger than the appendix bursae but in certain genera they can be more or less equal in size while in others, the latter can be significantly larger. In such cases it is necessary to locate the ductus seminalis to identify the structures. Similar to the ductus bursae, it is suggested herein to use descriptive terms to refer to the sclerotised and gelatinous structures in the corpus and appendix bursae.

The 11th female abdominal segment of Lithosiini, as well as of other Lepidoptera, is presumably represented only by the perianal membrane (Kristensen 2003a).

Comments

Editum

The term *plica centripetalis* was introduced by Birket-Smith (1965) for a mixture of structures: a costa, an editum and a lamella centralis, and is therefore unusable. Equally, Birket-Smith's (1965) terms '*processus basalia plicae*' and '*processus distalis plicae*' introduced for the proximal and medial processes of the valva cannot be used either as they refer to various processes of different origins.

Pierce (1909) introduced the term *editum* for a 'small finely spined prominence ... below the ampulla, on the costal side' while Kristensen (2003a) defined the editum as "an arched, setose prominence below the basal part of the costa". The editum *sensu* these authors refers to the structure, which is a part of the valval section of the transtilla (see below). Fibiger *et al.* (2009) called the editum the sclerotised and partly setose plate in Acronictinae (Noctuidae), which clearly refers to the 'sclerotised plate of annelifer' of Sibatani *et al.* (1954) and the *plica centripetalis* of Birket-Smith (1965) with regard the sclerotised fold, the ental extension of which is connected with its counterpart by the 'transtilla' *sensu* Forbes (1939). In the present paper the term ***editum*** is also accepted to refer to this sclerite on the inner surface of the valva, which represents a sclerotisation of the valval section of the transtilla.

In the Erebidae genital morphology illustration provided by Goater *et al.* (2003: 34), the elongate sclerite stretching along the costa and extended mesad as the ‘transtilla’ was indicated as the ‘clasper’, while it is definitely homologous to the editum *sensu* Fibiger *et al.* (2009), and Birket-Smith’s plica centripetalis (partim.).

In the majority of Noctuidae, the dorsal margin of the editum is fused with the ventral margin of the costa giving an illusion of the solid sclerite, which used to be considered as the costa. However, the longitudinal fold indicating the suture between these two sclerites (the *lacinia costae* of Sibatani *et al.* (1954)) is recognisable in most cases and, moreover, in certain groups their distal sections are separated from each other (Figs 48–59). In a number of genera, only the dorsal section of the editum (which is extended mesad into a tendon) is fold-like while its more ventral and distal regions are to a greater or lesser degree flat (Figs 48, 51); this may suggest the presence of another sclerite (similar or even homologous to the *lamella centralis* of the Lithosiini), which is however, unlikely, and in the present paper such flat sclerotisation in the Noctuidae is considered a part of the editum. Nevertheless, this question requires further extensive morphological studies involving a large number of genera.

In certain groups of the Noctuidae (e.g., some *Acronicta* Ochsenheimer, 1816 *s.l.*), similar to a number of Lithosiini, the editum is displaced dorsad and the basal section of the dorsal margin of the valva seems to belong to it while the dorsal end of the basis valvae is situated slightly more ventrally and the basal section of the true costa is situated on the outer wall of the valve.

With regard to the Lithosiini, Scott & Branham (2012) called two different, non-homologous structures the ‘editum’. Unfortunately, as the drawings provided by the authors are very schematic and the illustrated southern Nearctic Lithosiini species have never been dissected by the present author, it is currently impossible to identify those structures with certainty. Scott & Branham’s (2012: figs 31, 33) ‘proximal editum’ of *Lycomorpha fulgens* (H. Edwards, 1881) likely refers to the cluster of setae belonging to the true editum, which is fused with the costa into an editum-costa complex (similar to some Afrotropical genera of Lithosiina). The ‘distal editum’ in *Inopsis modulata* (H. Edwards, 1884), according to the schematic drawing of the valva (Scott & Branham 2012: fig. 35), belongs to the cluster of setae lying at the inner edge of the sclerotised formation referred to as the ‘clasper’ by the authors.

It is worth mentioning that the presence of setae cannot be used as a ‘diagnostic feature’ of the editum with any certainty, since in the Lithosiini, clusters of setae are located in various regions of the valva: not only on the editum but also on the costa, lamella centralis, valvula, and dorsal margin of the sacculus while the editum in certain groups is smooth or bears clusters of spinules.

Ental processes of valva

The term *tendon* was introduced by Forbes (1939) as a collective term for any ental extension of the valva serving as an insertion point for the *extensor of the valva* (muscle no. 4) and the *depressor of the peniculus* (muscle no. 3). The term *costula* introduced by Weller (1990) for Notodontidae and subsequently applied to Lithosiini by Bendib & Minet (1999) is obviously synonymous to the tendon *sensu* Forbes (1939). In most Erebidae and Noctuidae, Forbes’ ‘tendon’ refers to the ental extension of the editum but in certain groups it is not developed and an ental process of the costa serves as an apodeme instead. In the present paper the term ***tendon*** (= half of the *hemitranstilla sensu* Stekolnikov & Kuznetzov (1981)) is accepted in reference to the diaphragmal sclerotisation of the transtilla, which is in most cases an ental extension of the editum, while the ental process of the costa should be called the ***processus momenti***, following Birket-Smith (1965). The term processus momenti is preferred to Weller’s and Bendib & Minet’s *costula* because the latter in fact refers to the ental process of the editum while its name derives from the costa, which is somewhat misleading.

Transtilla

Pierce (1914) introduced the term *transtilla* within the Geometridae to refer to “a cross bar ... from the bases of the valvae” and also noticed that it “may be incomplete, the opposing arms not uniting, and whilst it is often simple, it is capable of great development, occasionally producing free arms [likely referring to the transtillar processes]”.

Busck & Heinrich (1921) followed Pierce and applied this term to Microlepidoptera, defining it as “a more or less band-like bridge connecting the harpes [valvae] at their inner costal angles”, and also noticed that it may be “attenuated or broken in the middle ... and appearing as free arms [=tendons] from the harpes [valvae]”, which “may be reduced to mere knobs or spurs”, and that “sometimes the transtilla is entirely absent". Forbes (1939) used the term transtilla in a more restricted sense to refer to the sclerotisation of the diaphragm above the anellus connecting two tendons. Birket-Smith (1965), following Forbes, also called the dorsal secondary sclerotisation of the diaphragm connecting the ental processes of the valvae as the 'transtilla', but the author specified that the processes connected by the 'transtilla' are the ental processes of the 'plicae centripetales' (refer to editum). Contrary to Forbes (1939) and Birket-Smith (1965) and similar to Pierce (1914) and Busck & Heinrich (1921), Stekolnikov & Kuznetzov (1981) called the 'transtilla' the continuous structure consisting of the ental processes of the 'costae' and the intermediate sclerotisation connecting them while for the 'interrupted transtilla' (i.e., the ental processes of costae, which are not connected by the secondary sclerotisation of the diaphragm), the authors introduced the term *hemitranstilla*.

In certain groups of Lithosiini, the tendon and sometimes even the editum are not developed but the fold stretching along the ventral margin of the costa and continued mesad into the diaphragm dorsad of the anellus is present. Taking this into account, it is logical to accept this fold as a basic (possibly, plesiomorphic) structure, which in most groups bears the secondary sclerotisations mentioned above, and accept the term ***transtilla*** to refer to it, while the terms ***editum*** and ***tendon*** are used to refer to its valval and ental sclerotisations, respectively.

Ampulla and digitus

The term *ampulla* was introduced by Pierce (1909) within the Noctuidae to refer to the process, which is independent of the clasper, arising from the inner surface of the valva between the clasper and the costa, and in fact is a process of the valval part of the transtilla. In Lithosiini and many other groups of Erebidae and some Noctuidae, the ampulla arises from the editum while in some Noctuidae the sclerotisation of the transtilla surrounding it can be very weak, the reason why Pierce (1909) and, subsequently, Sibatani *et al.* (1954) considered the ampulla and editum as two independent structures.

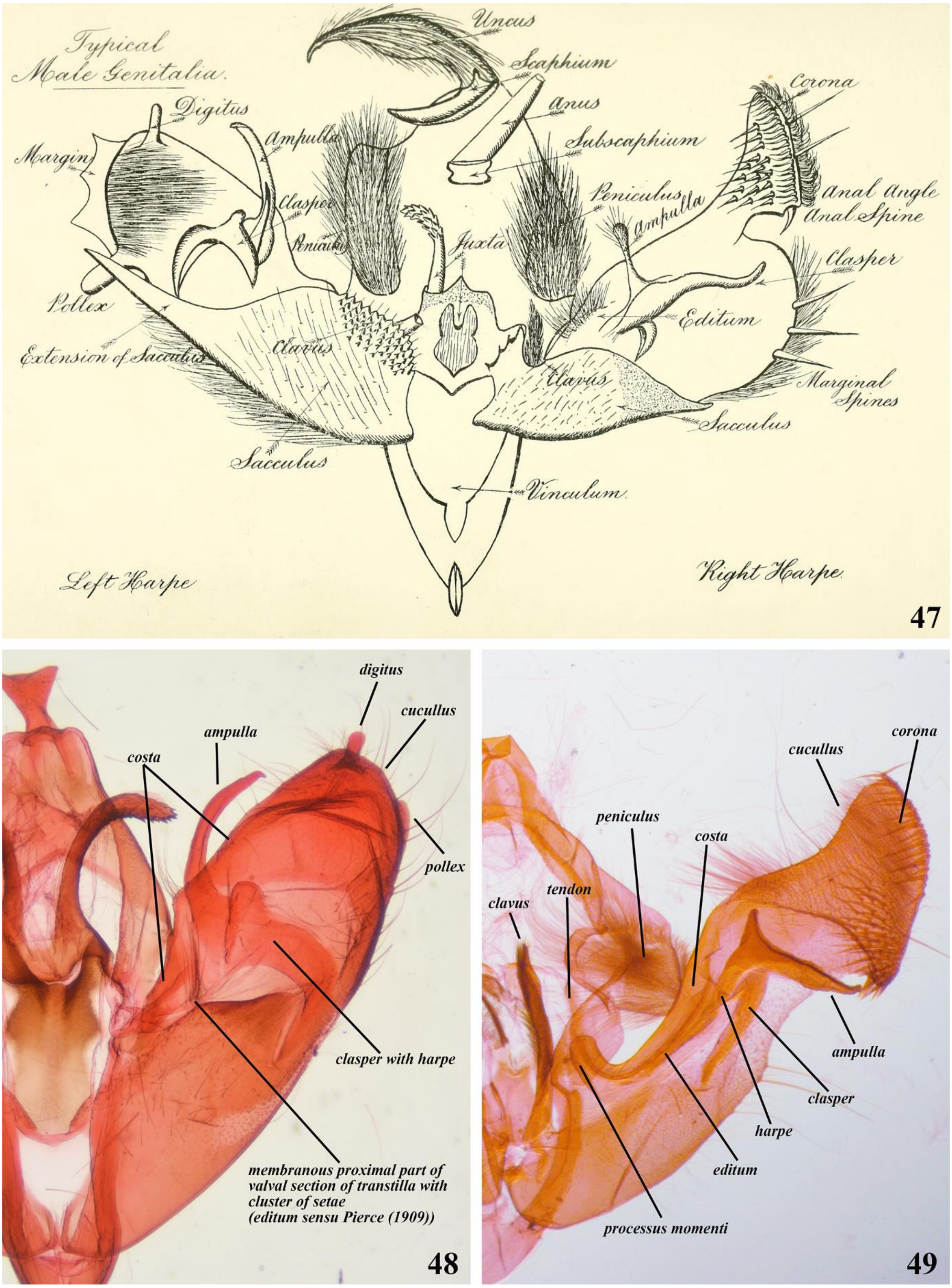
The term *digitus* was introduced by Pierce (1909) within the Noctuidae to refer to the process arising from the inner surface of the cucullus which is morphologically a distal section of the costa. In the original illustration by Pierce (1909) (Fig. 47) the digitus is indicated on the easily recognisable apex of the valva of *Orthosia gothica* (Linnaeus, 1758) (Noctuidae: Noctuinae: Orthosiini) (Fig. 48).

Subsequently Forbes (1934) erroneously identified those structures and started using the term 'ampulla' to refer to the dorsal process of the clasper while the term 'digitus' was used by the author to refer to the process, which morphologically is a distal-ventral extension of the editum (Figs 49, 50, 54).

As the costa and the editum have not been separated from each other by the majority of the authors, and the latter has been considered as a ventral region of the former, the terms digitus and costal process have been used in most cases to refer to the distal process of the editum/transtilla (e.g., Hacker 2004; Fibiger & Hacker 2007; Zilli *et al.* 2005, 2009; Fibiger et al. 2010; Ronkay *et al.* 2011, 2017) while the term ampulla has been correctly used to refer to this process only in cases of weak sclerotisation of the more proximal section of the transtilla (e.g., Sibatani *et al.* 1954; Fibiger 1997; Varga & Ronkay 2007).

Cucullus

It is also worth mentioning the term *cucullus*, of which there appears to be no consensus. In its strict sense, the cucullus is a distal section of the valva "of more or less separated shape" (Kononenko 2010), which is separated from the more proximal parts by the constriction called the *neck of cucullus*. This definition of the cucullus is mostly applicable to the male genitalia of some groups of Noctuidae (the tribes Hadenini, Leucanini, Apameini, etc.) (Figs 49, 55). In its wider (and original) meaning introduced within the Noctuidae by Pierce (1909), the term cucullus is used to refer to the distal region of the valva regardless of whether it is separated (e.g., Klots 1970; Fibiger 1997) (Figs 48, 50–54, 56–59). In addition to the aforementioned concepts, Scott & Branham (2012) and Volynkin (2023, in a more restricted sense) called the 'cucullus' a distal section of the costa in Lithosiini, which, however, can form a small process situated significantly more proximally than the tip of the valva, or be thin and fused with the dorsal margin of the valvula and thus naming the distal section of the costa as the cucullus cannot be generally accepted. It is suggested herein to avoid using the term cucullus in lichen moths as the structure of the distal section of the valva of Lithosiini is diverse and complex. The latter can consist of two or three different structures in different taxa; for example, the distal section of the valva of Lithosiini can be a complex of the terminal section of the costa and the *valvula*, or be the valvula alone, in which case it may bear an area of weak dorsal sclerotisation dorsally. Additionally, the distal extension of the sclerotisation of the sacculus can edge the distal section of the valva ventrally and distally.



Figures 47–49. Details of the male genitalia structures of Noctuidae. 47, the original plate by Pierce (1909); 48, subgenus *Semiophora* Stephens, 1829 of *Orthosia* Ochsenheimer, 1816, slide AV8579 (ANHRT); 49, *Amphipoea* Billberg, 1820, slide AV1662 (CAV).

Valvula

The term *valvula* was introduced by Pierce (1914) within the Geometridae to refer to "the central part of the valva, lying between the costa and the sacculus" and described it as follows: "It is in most cases composed of thin semi-transparent chitine, and is covered more or less with hair. As a rule the valvula is united to the costa and sacculus, but sometimes it projects free. Its outer margin is subject to extreme modification and ranges from an even curve to a deeply emarginate one". This term in its original meaning seems to be collective and belonging to a complex of formations. Sibatani *et al.* (1954) interpreted Pierce's definition of the valvula as "the distal, less strongly sclerotized part of the ... valva (perhaps including the cucullus in some forms)". This more restricted concept of the valvula was subsequently accepted for Lithosiini by Scott & Branham (2012), the term also being used in this sense by Kristensen (2003a), and is thus accepted in the present paper. With regard the Lithosiini, the valvula is suggested for use as a replacement term for the 'distal membranous lobe of valva' *sensu* Volynkin & Černý (2017b) and 'apical lobe of valva' *sensu* Volynkin & Černý (2016) (Figs 1, 10–19, 21–25).

Corona

The term was introduced by Pierce (1909) within the Noctuidae to refer to the "uniform row of incurved spines" on the outer margin of the cucullus and was widely accepted in this sense by later authors. This term was also applied to Lithosiini by Scott & Branham (2012)) in two modifications: the 'corona of seta' of *Archithosia s.str.* (incorrectly identified by the authors as '*Eilema bipuncta* (Hübner)') and the 'spined corona' of *Lycomorpha fulgens*. The latter is reminiscent of the true corona in Noctuidae as it consists of robust setae stretchinhg along the outer valva margin but both these clusters of setae are situated on the valvula while the corona of Noctuidae belongs to the sclerotised region of the cucullus, which is probably a continuation of the costal sclerotisation. Thus, the term corona is not applicable to the clusters of robust and almost undetachable setae on the Lithosiini valvula and therefore the new term ***iuba*** (nom. nov.) is introduced herein to refer to them.

Clasper region

The term *clasper* was introduced by Smith (1890) and was subsequently used by Pierce (1909) within the Noctuidae (subsequently replaced with 'harpe' by Pierce (1914) in the Geometridae) to refer to a sclerite in the middle of the inner surface of the valva (Fig. 47). Later, Forbes (1934, 1939) clarified its function as an insertion point of the massive intravalval muscle termed by the author the *flexor of the clasper*, or the *musculus gonopodalis internus medialis* (numbered as m_7) by Kuznetzov & Stekolnikov (2001) within the higher Lepidoptera, or the 'm. 5' of Birket-Smith (1965) within Lithosiina. In Noctuidae, Erebidae and Nolidae this muscle is mostly situated inside the sacculus and originates from the basis valvae or the ventral wall of the sacculus while its distal end is attached to the anterior side of the clasper in Noctuidae and Nolidae. As most members of Erebidae historically used to be considered as taxa within Noctuidae, the Noctuid terminology is traditionally applied for their genitalia strucutres. However, unlike Noctuidae, the genitalia of Erebidae display diverse modifications, and Fibiger & Lafontaine (2005) noticed that this caused problems in recognising and defining a number of structures, including the 'clasper'. For example, in the Erebidae genitalia morphology illustration provided by Goater *et al.* (2003: 34), the elongate inner sclerite stretching along the costa and indicated by the authors as the 'clasper' is apparently a transtilla with a tendon, an editum, and a well-developed and distally directed ampulla.

Limited studies of the male genitalia musculature of various subfamilies of Erebidae (e.g., Tikhomirov 1979a, 1979b, 1979c; Kuznetzov & Stekolnikov 2001) have shown that among the genera studied, only in *Catocala* Schrank, 1802 and *Lygephila* Billberg, 1820 does the intravalval muscle distally attach to the sclerite on the inner surface of the valva, which probably can be considered as the clasper, while in most groups of this family, the clasper *sensu* Noctuidae is absent and the intravalval muscle is attached to the area on the inner surface of the valva, which can be situated more or less medially (e.g., Hypeninae, Rivulinae, certain Herminiinae and Lithosiini) or displaced distally to the base of the distal saccular process (e.g., Aganainae, Calpinae, certain Herminiinae and Lithosiini) or 'cucullus' (e.g., certain Arctiini and Lymantriinae).

It is logical to accept the aforementioned membranous area of the attachment of the intravalval muscle as a basic (possibly, plesiomorphic) structure (the ***clasper region***, nom. nov.), which may bear a sclerite called the clasper in Noctuidae and certain Nolidae and Erebidae (similar to the editum, which is a sclerotisation of the transtilla). This assumption is supported by the example of the reduction of the clasper in certain species of the genus *Noctua* Linnaeus, 1758 (Fig. 56), in which the clasper region is broader than the anterior margin of the clasper. This size discrepancy and the reduction of the clasper, which is thin and weakly sclerotised, apparently led to Forbes' (1934) incorrect conclusion that the pollex of the '*Noctua* group' is the clasper.

Saccular processes in Lithosiini

In a number of genera of the subtribe Lithosiina as well as certain genera of Nudariina (e.g., *Cyana*) the clasper region is situated near the base of the heavily sclerotised and distally directed process termed by various authors as the 'distal saccular process' (e.g., Holloway 2001; Volynkin 2016) or 'ventral process of valva' (Dubatolov & Zolotuhin 2011). Following Forbes' (1934, 1939) concept of the clasper, the suggestion to call the distal saccular process of Lithosiini as the 'clasper' by Witt *et al.* (2011), as well as Birket-Smith's (1965) suggestion to call the 'distal saccular process' of the Lithosiini as the 'harpe' (the process of the clasper in Noctuidae: see below) may seem reasonable. However, in other groups of Lithosiini (as well as in a number of other Erebidae subfamilies) the clasper region is situated on the inner wall of the valva and is membranous while the ventral sclerotisation of the valva, which is a continuation of the saccular 'pocket', is still present and terminates with a distal process, which is highly likely homologous to the process at the base of which the clasper region is situated in other groups. Thus, terming the ventro-distal process of the Lithosiini valva as the 'clasper' or 'harpe' is apparently incorrect.

Kuznetzov & Stekolnikov (2001) termed a distal process of the sacculus of the Lepidoptera as the *cuiller* and applied it also to the Lithosiini. Nevertheless, this term is not used in the literature devoted to the Noctuoidea and it is therefore not accepted in the present paper. Another Noctuidae term, the use of which should be avoided in the Lithosiini, is the *clavus* introduced by Pierce (1909) to refer to the ventral and setose process or the setose area on the dorsal side of the proximal section of the sacculus (Figs 47, 49–51). It appears as a sensillae-bearing structure and therefore is most probably non-homologous to the smooth basal saccular process of the Lithosiini.

With regard the Lithosiini, it is suggested herein to use descriptive terms to refer to the processes of the sacculus of Lithosiini, such as ***distal, dorsal*** or ***basal*** **(*proximal*)** ***saccular processes***.

Harpe and pollex in Noctuidae

The term *harpe* was introduced by Gosse (1883) within the Papilionidae to refer to a process on the inner surface of the valva, which is probably homologous to the ampulla of Noctuidae and Erebidae. Smith (1890) used this term within the Noctuidae to refer to the valva (in its current meaning), which was followed by Pierce (1909) and later by Busck & Heinrich (1921) despite Pierce (1914) replacing the term 'harpe' with 'valva' and applying the term harpe to the clasper within the Geometridae.

In a number of groups of Noctuidae the clasper is represented not just as a sclerotised plate but bearing one or a few processes, of which there is no consensus regarding its terminology. In most cases the clasper bears a single process arising from its dorsal part and directed dorsally or dorso-distally which Forbes (1934) called the *ampulla*, unlike the original meaning of this term by Pierce (1909). Later, Forbes (1939) did not use the term 'ampulla' and did not distinguish the process as a special term and called the whole structure the 'clasper'. Sukhareva (1973) stated that it was advisable to limit the concept of the clasper to the sclerite only while its process (ampulla *sensu* Forbes (1934)) should be called the *harpe*, as suggested by Rjabov (1951). In a number of subsequent publications devoted to Noctuoidea, there has been no consensus and the process of the clasper was called either a harpe (e.g., Lafontaine 1987; Hacker 2004; Kononenko 2010), or ampulla (e.g., Forbes 1954; Zilli *et al.* 2005; Mikkola *et al.* 2009), or, following Pierce (1909) and Forbes (1939), the whole plate/process complex was called the 'clasper' (e.g., Lafontaine & Poole 1991; Fibiger 1997; Lafontaine 1998). Additionally, in the literature there are further examples of the use of the term harpe in Pierce's (1914) and Forbes' (1939) concept of the clasper (the plate + the process) (e.g., Varga & Ronkay 2007; Varga *et al.* 2015). As the term ampulla refers to the process of the transtilla/editum, and as in a number of Noctuidae species the clasper is plate-like and lacks process(es), it seems logical to accept the concept by Sukhareva (1973) and use the terms clasper and harpe to refer to the plate and its dorsal free process, respectively (Figs 48, 50, 51, 53–59).

The term *pollex* was introduced by Pierce (1909) in the Noctuidae to refer to the "projecting column or thumb" situated on the ventral side of the cucullus, which is *a process of the ventral margin* *of the valva*. The pollex is independent from the clasper and these two structures are remote from each other in such groups as Orthosiini (Fig. 48), Tholerini (Fig. 58) and certain Noctuini (Fig. 56) while in some genera (e.g., *Xestia* Hübner, 1818) the clasper is displaced more distally and its distal protrusion is situated very close to and sometimes even articulated with the pollex. For this reason Forbes (1934) erroneously characterised the pollex as an extension of the 'ventral arm of the clasper'. This confusion in the interpretation of terms caused problematic statements in the literature, e.g., the ventral process of the cucullus of Orthosiini correctly being called the pollex by Ronkay *et al.* (2001) but later being referred to as the 'pollex-like process' of the cucullus by Ronkay *et al.* (2010). Due to Forbes' aforementioned erroneous identification, it has been widely accepted in the recent literature by, for example, Hacker (2004), Fibiger & Hacker (2007), and Fibiger *et al.* (2009), who used the term pollex to refer to the true ventro-distal extension of the clasper of Xylenini and Acronictinae.

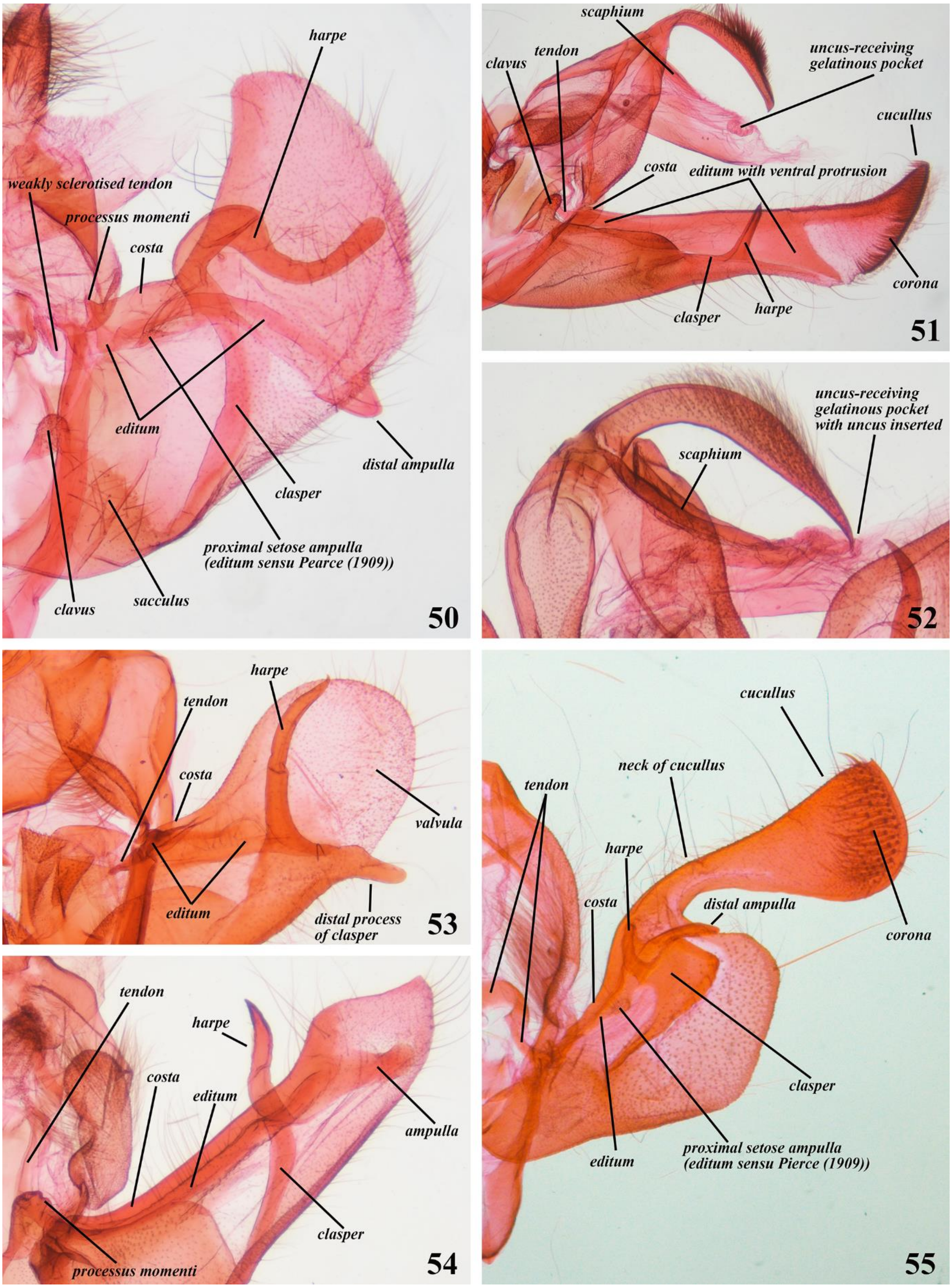
Varga *et al.* (2015) defined the pollex of *Xestia* as a "ventral extension originating from the sclerotised base of the harpe ("clasper" in Lafontaine) that projects below the ventral margin of the valva". However, within *Xestia* the relative position of the clasper and the pollex is diverse and these structures can be separated, articulated or overlapping (Figs 59–64), and it is clear that the latter cannot be considered as an extension of the former, as cases of articulation of the clasper and the sacculus are widespread among Noctuidae and some Erebidae, and they are not a proof that the clasper is an extension of the sacculus.

In contrast to their concept of the pollex in *Xestia*, Varga *et al.* (2015) introduced the new term "*pseudopollex*" to refer to the ventral process of the valva of the so called '*Eugnorisma* Boursin, 1946–*Eugraphe* Hübner, 1821 generic complex', and defined it as a possible "modified saccular extension, derived from the distal end of the sacculus". Nevertheless, despite the ventral (saccular) sclerotisation of the valva reaching the base of the "*pseudopollex*" in certain genera of the aforementioned generic complex (e.g., in *Schizognorisma* L. Ronkay & Varga, 1999, *Protognorisma* L. Ronkay & Varga, 1999, *Anagnorisma* L. Ronkay & Varga, 1999, and certain *Eugnorisma* (Fig. 57)), the "*pseudopollex*" is mainly formed by the distal sclerotisation of the valva extending into the outer wall of the valva, and separated from the saccular sclerotisation by a membranous region (e.g., in *Opigena* Boisduval, 1840). This is clearly the true pollex homologous to those of other Noctuini (e.g., *Xestia*, *Noctua*) as well as other subtribes of Noctuinae such as Orthosiini and Tholerini, while the true distal saccular process is also present in the '*Eugnorisma-Eugraphe* generic complex', namely in the genus *Afrognorisma* Varga, G. Ronkay, L. Ronkay & Gyulai, 2015.

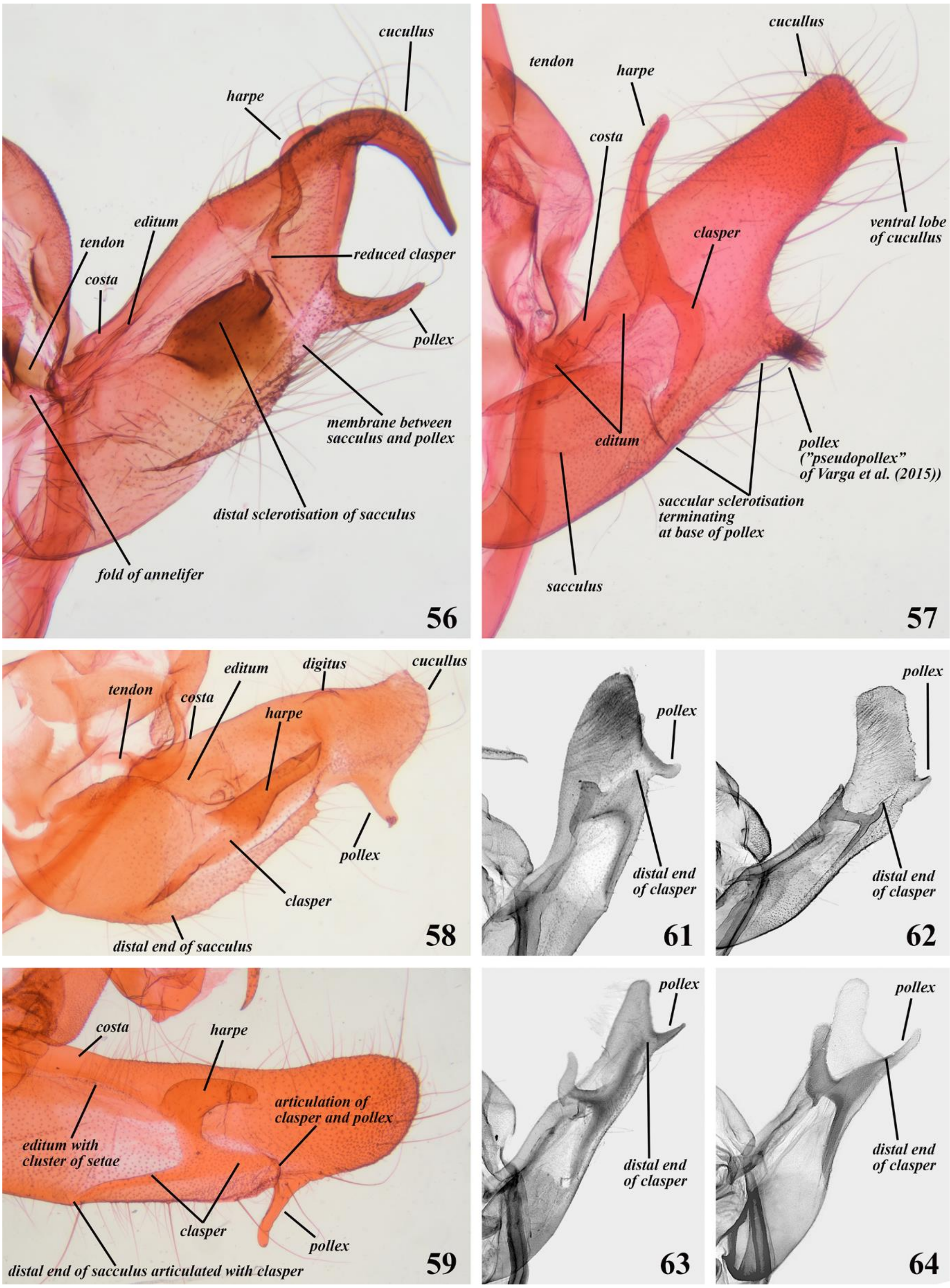
Valvellae

Birket-Smith (1965) introduced the term ***valvella*** to refer to the paired sclerotised process- or lobe-like structure situated in the periphallic region laterad or dorso-laterad of the phallus. Similar to some other terms introduced by this author, the 'valvella' is a collective term in fact referring to the processes of three different origins.

(1) The largest group of 'valvellae', which Birket-Smith found in various non-related families (Birket-Smith 1965, 1974a, 1974b), are processes of the juxta (Kinazawa 1987; Kristensen 2003a), which can arise dorso-laterally (Fig. 25) or laterally. A good example of the latter is the lateral lobes of the genus *Zobida* Birket-Smith, 1965, which are strongly enlarged, heavily sclerotised and dentate, and are laterally fused with the annelifer while the medial section of the juxta connecting them is flat, smooth and weakly sclerotised. In many cases (e.g., in *Zobida*, *Archilema* Birket-Smith, 1965) the process of the juxta is an insertion point for the inner muscle of the juxta, which was identified by Kuznetzov & Stekolnikov (2001) as the '*inner secondary muscle of the median plate*' (the *musculus laminae mediale novus internus*, m_{31}) while Birket-Smith (1965) numbered this muscle as 'm. 11'. Kristensen (2003a) assumed the aforementioned juxtal muscle is a derivative of the primary muscle *sIX-mep* originating from the vinculum and inserted into the juxta, but Kuznetzov & Stekolnikov (2001) treated Kristensen's *sIX-mep* as one of the two variants of the primary *musculus laminae mediale anterior* (m_3) while another variant is the muscle proximally attached to the base of the sacculus and called by Kristensen *mep-vlv*. Contraction of both kinds of muscles abduct the valvae but in different ways (described in detail by Kuznetzov & Stekolnikov 2001): the *mep-vlv* works is a direct abductor while the *sIX-mep* creates mechanical tension at the junction of the base of the juxta and the sacculi, causing the valvae (articulated with the juxta) to automatically spread apart. In light of this, Kristensen's concept of *mep-vlv* and *sIX-mep* being two different primary muscles, not just two variants of the same one appears more justified.



Figures 50–55. Details of the male genitalia structures of Noctuidae. 50, *Dasypolia* Guenée, 1852, slide AV7482 (CAV); 51, *Cucullia* Schrank, 1802, slide AV7508 (CAV); 52, *Acronicta* Ochsenheimer, 1816 (*s. str.*), slide AV7509 (CAV); 53, subgenus *Simyra* Ochsenheimer, 1816 of *Acronicta*, slide AV0368 (CAV); 54, subgenus *Xandria* de Laever, 1983 of *Leptologia* Prout, 1901 (ANHRT); 55, *Mythimna* Ochsenheimer, 1816, slide AV1283 (CAV).



Figures 56–64. Details of the male genitalia structures of Noctuidae. 56, *Noctua*, slide AV8580 (ANHRT); 57, *Eugnorisma* Boursin, 1946, slide AV7514 (CAV); 58, *Cerapteryx* Curtis, 1833, slide AV0551 (CAV); 59, *Xestia*, slide AV1756 (CAV); 61–64, *Xestia* spp. (photo by V.S. Kononenko).

Taking this into account, Kuznetzov & Stekolnikov's (2001) treatment of Birket-Smith's 'm. 11' as the secondary inner muscle of the juxta seems to be most logical and is therefore accepted herein.

(2) The ‘valvellae’ of genera such as *Cragia* Birket-Smith, 1965, *Aroterosia* Krüger, 2015, *Muxta* Birket-Smith, 1965, *Pseudocragia* Krüger, 2015, *Cragandhara* Volynkin, 2023, *Gandhara* Moore, 1878, *Lobilema* Aurivillius, 1910, *Pseudochromatosia* Krüger, 2015, and *Campteropsis* Krüger, 2016 are the sclerotised processes of the anellus. As such processes remain unnamed it is herein suggested that the term ***valvella*** should be used to refer to them. The valvellae are situated laterad, ventro-laterad, or dorso-laterad of the phallus, and form an integrative part of the intromittent complex. According to Birket-Smith (1965), in *Cragia* (Figs 26, 27) (and most probably in *Aroterosia* as it is morphologically very similar) the valvellae are insertion points of the muscle originating from the ventro-lateral processes of the juxta. This muscle may be a derivative of the inner secondary muscle of the median plate but clarification of this requires further studies. The contraction of this muscle apparently bends the ‘valvellae’ downwards, and these processes possibly perform the function of opening the female ostium bursae during copulation; this assumption is confirmed by the structure of the female antrum in *Cragia* and *Aroterosia*, which bears pockets apparently designated for receiving the valvellae (similar to the correspondence of the male juxta and female antevaginal plate discussed by Mikkola (2008) as an example of a part of the lock-and-key mechanism). In *Muxta*, Birket-Smith (1965) found no muscles inserted into the valvellae, which are smaller and weakly sclerotised in this genus and it is also highly likely true for *Pseudocragia*, which is morphologically almost indistinguishable from *Muxta*. In these two genera the bases of the valvellae are fused with the phallic tube wall and the detachment of the phallus is possible only by cutting it out using Vannas Scissors. In *Cragia* and *Aroterosia* the sclerotisations of the bases of the valvellae are not fused but articulated with the adjacent regions of the phallic tube wall making the detachment of the latter from the phallocrypt problematic, although possible in most cases. The musculature of the periphallic regions of *Cragandhara*, *Gandhara*, *Lobilema* (Fig. 31), *Pseudochromatosia* and *Campteropsis* have never been studied. In the latter two genera, the valvella is situated dorso-laterad of the phallus and is a tongue-like fold of the anellus with a membranous dorsal wall while its ventral wall, as well as the lateral margins are heavily sclerotised and armed with denticles (Fig. 30). The females of these taxa have heavily sclerotised and rugose postvaginal regions of the sterigma apparently serving as an attachment place for the valvellae.

(3) In the genus *Archithosia* Birket-Smith, 1965 *s.l.* (Fig. 24), the ‘valvella’ arises from the sacculus and not the periphallic region. Birket-Smith (1965) noticed this but stated that the process is still the true ‘valvella’ arguing that the “dissection of the male genitalia ... demonstrating the nerves shows that the valvellae are not mere outgrowths from the base of valva, but true valvellae”. In the figure provided by the author (Birket-Smith 1965: fig. 6), the nerve ‘ae’ innervating the muscle ‘m. 10’ (Kristensen’s *mep-vlv*, and Kuznetzov & Stekolnikov’s *musculus laminae mediale anterior* (m_3), partim.) has a branch inserted into the process. However, no further explanation was provided by Birket-Smith (1965) and it remains unclear why the presence of that nerve branch is evidence of the process being the true ‘valvella’. It is possible the presence of the aforementioned nerve branch was considered by Birket-Smith (1965) as evidence of the reduction of the muscle ‘m. 11’ (Kuznetzov & Stekolnikov’s *musculus laminae mediale novus internus*, m_{31}), but such an assumption requires more investigation. Morphologically, the process of *Archithosia s.l.* is undoubtedly a part of the sacculus and it is herein considered as a basal saccular process.

Corethrogyne

The term was introduced by Diakonoff (1939) for Tortricidae and has also been applied to certain groups of Lithosiini by Holloway (2001), in reference to the dense tuft of highly modified hair-like scales bordering the ovipositor ventrally. It is found in a few genera of the subtribes Nudariina (e.g., *Miltochrista* Hübner, [1819] and *Arctelene* Kirti & Gill, 2008) and Cistheniina (e.g., *Siccia*).

Detachment of phallus and vesica evertion

The phallus partly turns outward from the phallocrypt during copulation, and it can be fully removed from the phallocrypt during dissection when pulled outward with forceps in the caudal direction (Fig. 11). In this instance, the sclerotisations of the anellus and the manica as well as the valvellae remain attached to the genital capsule (Figs 27, 28, 30) allowing them to be distinguished from the sculpture of the phallic tube, which is important as they attach to different parts of the female genitalia during copulation and therefore the placement of those sclerotisations may be taxonomically informative. This makes the aforementioned way of detaching the phallus preferable. Females of taxa with males having processes of the juxta, valvellae and carina have equivalent structures for them such as an antevaginal plate or pockets of antrum, and those male structures can serve not just for precopulatory attachment to the female abdomen but for opening the ostium bursae during copulation. Similar assumptions concerning the function of similar male processes have already been made for Zygaenidae (Fänger & Naumann 1997) and Geometridae (Mikkola 1994; Sihvonen & Mikkola 2002).

It is necessary to mention the importance of the examination of the vesica structure for the purposes of taxonomy. The male phallus and vesica, and the female bursa copulatrix, together form a 'lock-and-key mechanism', which play the role of specific reproductive isolation (discussed in detail by Mikkola (2008)). The vesica configuration and ornamentation are species-specific and in many genera and species-groups the reliable morphological differences can be found only in the vesica structures. Thus, the evertion of the vesica is essential for species delimitation and identification. It was problematic in the past due to the availability of fine tools but at present, the technique of evertion is well described in the literature (Lafontaine & Mikkola 1987; Dang 1993; Mikkola 2007; Kononenko 2010), and 34-gauge syringe needles are easily obtainable making the evertion of the vesicae of even small moths a standard procedure. However, some of the important taxonomic papers published relatively recently (e.g., Karisch 2013; Krüger 2015, 2019; Spitsyn & Bolotov 2020) lack data on the vesica morphology (except for the number and size of the cornuti visible through the phallus wall) and are mostly based on the external morphology of moths and their male genital capsules. In one of the aforementioned papers devoted to the South African genus *Entephrilema* Krüger, 2015 (Krüger 2019), 38 new species displaying nearly no differences in their genital capsules were described without examination of the vesica structures, which has created a serious problem for future studies of the genus.

Conclusions

Since Birket-Smith's (1965) publication, there have been no treatments devoted to the morphology of the genitalia structures of lichen moths. Birket-Smith introduced a number of new terms within the Lithosiina, but unfortunately, as discussed above, some of them are collective terms and refer to structures of different origins. As no homologies with other groups of Noctuoidea have been discussed by the author, the applicability of many of Birket-Smith's terms is very limited as Lithosiini belong to the family Erebidae and the genitalia terminology of the tribe has to be consistent with that of the Erebidae in general. This is crucial in terms of phylogenetic studies, which require the correct identification of various morphological structures in order to recognise homologies and trace their modifications in related groups.

As members of the family Erebidae were long considered as noctuid moths, the Noctuidae genitalia terminology is traditionally applied to the Erebidae. However, the Noctuidae genitalia terminology has, in fact, limited applicability to Erebidae as in the latter, the genitalia are highly diverse in their structure with certain characters either not present in Noctuidae or their homology highly dubious. The present paper takes into account the most important works devoted to the Noctuidae and Erebidae genitalia morphology and provides a more or less full overview of the genital structures observed by the author in various groups of Lithosiini. Some of these characters were found to be nameless in terms of the widely accepted Noctuidae genitalia terminology, which necessitated the introduction of several new terms, some of which may also apply to the Erebidae in general. Nevertheless, as the genitalia structures of many other subfamilies and tribes of Erebidae are significantly different from Lithosiini, additional extensive morphological studies with potential introductions of further new terms are highly desirable for this extremely speciose and diverse family.

Although the genitalia of Noctuidae are more uniform and simple than those of Erebidae and a number of the basic terms were originally introduced for this family, the Noctuidae genitalia terminology is currently controversial and confusing as different authors term the same structures in different ways while also applying the same terms for non-homologous structures. In the present paper, a few such terms are discussed with reference to the original concept by the various authors who introduced them, and the approaches by authors *sensu auct.* are also considered. Since the current Noctuidae genitalia terminology is mainly based on the knowledge of the Holarctic fauna, further studies involving numerous taxa from other geographic realms are necessary; however, it is believed that the attempt by the present author to clarify some terminological inconsistencies may prove useful for future studies of the family.

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