FUNCTIONAL MORPHOLOGY OF THE MALE GENITALIA AND THE PHYLOGENETIC

RELATIONSHIPS OF SOME PRIMITIVE SUPERFAMILIES OF THE INFRAORDER

PAPILIONOMORPHA (LEPIDOPTERA: SESIOIDEA, COSSOIDEA, ZYGAENOIDEA)

OF THE ASIATIC PART OF THE U.S.S.R.


(Funktsional'naia morfologiia genitalii samtsov i filogeneticheskie

otnosheniia  nekotorykh  primitivnykh  nadsemeistv,  infraotriada

Papilionomorpha (Lepidoptera:  Sesioidea, Cossoidea, Zygaenoidea)

fauny aziatskoi chasti SSSR).

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# EDITOR'S PREFACE

This paper is one of the few serious evaluations of higher classification of Cossoidea and Zygaenoidea. Specifically, it describes the male genital structure and musculature of the following taxa, as well as discussing their relationships to each other:

Choreutidae: Anthophila, "Eutromula" [now Choreutis montana], "Choreutis" [now Prochoreutis ultimana], Tebenna.

Sesiidae: Pennisetia, Zenodoxus, Paranthrenopsis, "Aegeria" [now Synanthedon flaviventris], Sesia.

Cossidae: Cossus, Dyspessa, Phragmataecia, Zeuzera.

Limacodidae: Monema, Latoia, Narosoideus, Cochlidion [now a synonym of Apoda], Apoda.

Zygaenidae: Zygaena, Balataea, Illiberis, Elcysma, Pryeria.

This paper was originally translated for the National Museum of Natural History, Smithsonian Institution, by Saad Publications, Karachi, Pakistan. The original English version was very awkward; I have attempted to make it readable without changing any meanings. I thank Don Davis (Smithsonian Institution) for arranging for the translation, George Steyskal (U.S. Dept. of Agriculture) for clarifying some difficult passages, and Tina Kuklenski-O'Connell (Bishop Museum) for word processing many drafts.

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In the recently published new classification of Lepidoptera (Kuznetsov and Stekol'nikov, 1978b), the gigantic infraorder Papilionomorpha (Dytrisia) takes a special position as the most flourishing group. The name of the infraorder is formed from Papilionidae, as the name of family rank based on _Papilio_ L. as suggested for the first time by Latrielle (1802-1803), and even earlier (Laicharting, 1781) it was suggested to name the whole order Lepidoptera as Papilionoides.

The number of superfamilies forming Papilionomorpha, the study of which is extremely necessary for comprehending the ways of evolution and clarifying phylogenetic relations within the infraorder, has not been touched until recently by special morphofunctional investigations.

The aim of the present article is to review the functional morphology of the male genitalia in 3 archaic superfamilies (Sesioidea, Cossoidea, and Zygaenoidea) and, by taking into account also other adult structures (and sometimes structures of pupae and larvae as well), to appraise their phylogenetic position.

The main material has been assembled and fixed in the south Primorie (Gornotaezhnaya stantsiya in vicinities of Ussuriisk and in the National Park Kedrovaya Pad). Additionally several species were assembled in the European part of the USSR. Specimens investigated were of Choreutidae, Zygaenidae and Limacodidae (1 species from 5 genera of each family), Sesiidae (5 species from 4 genera) and Cossidae (1 species each from 4 genera). The total number of genera investigated reached 23.

Nomenclature of muscles is the same as in our preceding publications (Kuznetsov and Stekol'nikov, 1978a, 1978b).

# REVIEW OF FUNCTIONAL MORPHOLOGY OF MALE GENITALIA

## IN SPECIES INVESTIGATED

### Family Choreutidae

Anthophila fabriciana L. (Fig. 1A, B). Type species of the large Holarctic genus Anthophila Hw. Tergal complex of genital appendages of this species includes, attached to distal angles of tegumen, an unpaired firmly sclerotized gnathos and lamellate uncus, apparently mainly implementing the tactile function. From the socii its membranous edges are fitted with setae, and muscles m1 are attached exactly to them. Such attachment of muscles is typical for Tortricidae and Oecophoridae possessing socii. Muscles m2 were not found.

Sternal region of the 9th segment is represented by a narrow vinculum, on which a bulky saccus is formed medially. Valvae, articulated with the vinculum, include well developed muscles m7 and are proximal to each other in the region of sacculi. Sclerotized zone between these valvae parts serves as attachment place of muscles m3, which thereafter approach to upper region of juxta.

Muscles m4 begin at the apex of saccus and hence extend to the upper bases of valvae, where they are fixed to small basal processes. In the costal region of the valvae the aedeagus protractors (m5) attach.

Eutromula montana Danil. (Fig. 1B) - near to the type species of the Holarctic genus Eutromula Frol. Just as in A. fabriciana L., the socii are developed in this species. However, the whole tergal complex is reduced: the tegumen is narrow, the gnathos has disappeared, and the uncus is represented by a membranous hood, concealing the top of the anal cone; muscles m1 are lost. The vinculum is quite broad. Attached on it are muscles m6, leading to aedeagus, muscles m4, which then approach the narrow basal process, and muscles m2, linking vinculum with juxta. Muscles m5, leading from basal projection of aedeagus, implant into the base of superior valvae region. Intravalvar muscles developed.

Attention is drawn to the functional asymmetry of the aedeagus, arising as a result of the aedeagus twisting at 180° along the longitudinal axis. The seminal duct enters into the sexual organ from underneath, and the muscles m5, leading from basal projection, are twisted. Muscle, fixed to basal growth on the right, passes under aedeagus and goes to left valva, while the left muscle above the aedeagus passes to the right side.

Choreutis ultimana Krul. (Fig. 2A) differs quite intensely from the type species of genus Choreutis Hb. This widely distributed genus includes many species. Ch. ultimana Krul. differs from the preceding species by the presence of small muscles m10, leading from tegumen to the base of subanal plate, absence of functional asymmetry of the aedeagus, and the extremely vigorous development of intravalvar muscles m7. The latter have come out beyond the sacculi, filling practically the whole cavity of the valvae. Muscles m4 lead from the base of saccus to superior basal angle of valvae, where the aedeagus protractors (m5) also attach. Muscles m3

connect the medial region of vinculum with the apex of juxta. The juxta is represented by an extended triangular sclerite with a medial rigid rib and is separated from the anellus.

In C. ultimana Krul., just as in E. montana Danil., the tergal region is considerably reduced - gnathos and muscles m1 are absent and the uncus is membranous and forms socii.

Tebenna caucasica Danil. (Fig. 2B) - recently described species (Danilevsky, 1976), near to the type species of the genus Tebenna Billb. This genus is well represented everywhere, except Australia and South America. T. caucasica Danil. shows the furthest stage of specialization of Choreutidae genitalia. The tergal region is extremely reduced, however, the socii are retained. Muscles m4 are absent in the sternal region. The valvae are opened by muscles m3, which are attached on vinculum and juxta, which represents a forward directed hollow sclerotized projection. The base of the juxta is articulated with the valvae bases. The valvae shift as a result of contraction of intravalvar muscles (m7). With this the pointed distal growths of the valvae firmly fix the position of the female abdomen. The attachment of muscles m7 to the superior sclerotized edge of the valvae and their shift in beyond the limits of sacculi is an unusual position for these muscles, which once more emphasizes the extreme specialization in the genitalia of T. caucasica Danil.

The aedeagus has a well developed basal growth, attached to which are the muscles m5. These muscles are attached by the other end to superior basal region of valvae. Muscles m6 lead from the medial projection of the vinculum to the dorsal process of the aedeagus behind the entry point of the seminal duct into aedeagus tubule.

## Family SESIIDAE

Pennisetia hylaeiformis Lasp., Tinthiinae (Fig. 3 A, B). Type species of the small and, probably, relict genus Pennisetia Dehne; which serves as type genus of the small tribe Pennisetiini, having a disjunct Palaearctic distribution range.

The 9th segment in this species is represented by a narrow faintly developed tegumen, articulated with similarly narrow lateral parts of the vinculum. A massive saccus is formed medially on the vinculum.

The uncus is weakly developed and carries on the sides small lobules, covered by setae. To these lobes (socii) come up muscles m1. Besides these muscles, another 2 pairs are found in the tergal region of the genital segment: retractors of anal cone (m10), linking tegumen with subanal plate, and muscles not described previously in Lepidoptera, located within the anal cone (m20 - m. subanalis). The presence in the anal region of 2 pairs of muscles is an extremely ancient character.

The valvae in P. hylaeiformis Lasp. are lamellate, broad, with clearly expressed basal processes. To each of them approach from above the tegumen extensor muscles (m2) and from below the vinculum valvae flexors (m4). In the region of sacculi the valvae are bound one with another by an inflated sclerotized region. To

5

the intravalvar sclerite approach from the juxta quite powerful muscles m3. Within the valvae the intravalvar muscles (m7) are developed.

The aedeagus has a clearly formed basal projection, from which lead muscles m5, pushing out the sexual organ. Muscles m5 are attached by their second end to aedeagus. The aedeagal retractor (m6) extends from the upper lateral part of the aedeagus to immediately after the entrance of the seminal duct into the aedeagus and then proceeds to the saccus.

Zenodoxus editha Butl., Tinthiinae (Fig. 3 C,D). Typical species of a small relict genus with a disjunct geographic range, Zenodoxus Grote and Rob., included in archaic tribe Tinithiini. Some taxonomists (Naumann, 1971) isolate this species into the independent genus Paranthrenopsis Le Cerf, however, the venation of its wings is exactly the same, and the structure of its genitalia is very similar to that of Zenodoxus tineiformis Esp. Therefore we leave it in the genus Zenodoxus Grote and Rob., distributed in the Holarctic and South Asia.

Genitalia of Z. editha Butl., are somewhat different from those of Pennisetia hylaeiformis Lasp., possessing at the same time a number of common features. Tegumen is more developed than in P. hylaeiformis Lasp. and articulated with well developed beak-like unpaired uncus. Socii are absent. The uncus is inclined downward as a result of contraction of muscles m1. The muscles of the anal region were, unfortunately, not investigated due to insufficient material.

The vinculum has an extensive saccus, to which are attached distally the powerful aedeagus retractors (m6) and proximally the thinner sternal valvae extensors (m3), leading from juxta. The attachment of muscles m3 in Z. editha Butl. sharply differs from their position in P. hylaeiformis Lasp. The other difference in Z. editha Butl. genitalia is the position of aedeagus protractors (m5). These muscles, starting at the end of aedeagus basal growth, became deeply implanted in the valvae.

The position of aedeagus retractors (m6) is unique. Leading away from the apex of saccus, these muscles split into two pairs of muscular fascicles prior to their attachment to aedeagus. One pair of muscles m6 attaches directly to aedeagus from above, close to the seminal duct. Fibers of the second pair of muscular fascicles m6 attach behind the first pair of anellus.

Muscles m7 are developed within the valvae and cover the sacculus. The valvae are activated by muscles m2, which extend from the dome of tegumen to small basal processes. Muscles m4 were not actually found, however, their presence is assumed with a high degree of probability.

Sesia apiformis Cl., Sesiinae (Fig. 4). Type species of the small Holarctic genus Sesia F. This genus is the type genus of the tribe Sesiini.

Genital apparatus of S. apiformis Cl. is represented by a dome-shaped tegumen, leading from which is a strong gnathos. Articulated with tegumen is a paired appendage, fitted along the edges with chaetae. It is assumed that this formation has arisen on the bases of socii, similar to those of Pennisetia hylaeiformis Lasp. These lobes became hypertrophied, having taken on for the second time mechanical function. Approaching the base of the lobes are their depressors (m1). Moreover, in the tergal region of the 9th segment the retractors of the anal cone (m10) are developed. Muscles m2, represented in the previously examined S. apiformis Cl., are absent.

Narrow vinculum is articulated with lobe-shaped valvae, provided with muscles m7. Approaching upper angle of valvae bases are powerful flexor muscles m4. The additional flexor function of valvae is implemented by the aedeagus protractors (m5), which lead away from the basal growth of aedeagus and then are implanted within the valvae, attaching to their external wall. Opening of the valvae is ensured by their sternal extensors (m3), connecting the upper anterior angles of juxta with the upper edge of saccus.

The position of aedeagus retractors is the same as in P. hylaeiformis Lasp.

Aegeria flaviventris Stgr., Sesiinae (Fig. 5). Typical species of the large and widely distributed Northern Hemisphere genus Aegeria F., which serves as a type genus for the tribe Aegeriini.

Genitalia of this clearwing moth possess a unique appearance, imparted to them by modified tergal region. The tegumen has on the sides a membranous window and because of this its dorsal part is frequently regarded as uncus (Naumann, 1971; Fibiger and Kristensen, 1974). Judging from the position of m1, this species has no uncus. Tegumen on sides transmits into unusual gnathos, represented by 3 longitudinal lamellate sclerotized lobes. Moreover, the posterior angles of the tegumen are fused with a pair of membranous growths, densely covered by accumulation of androconial hair (scopula androconialis). Since muscles m1 approach the base of the growth, we regard all of these formations as the whole socii, and not only their basal parts, as assumed by some investigators (Naumann, 1971). The position of muscles m10, which lead from tegumen to anal cone, does not differ from the ancestral scheme.

Tegumen is articulated with narrow vinculum, from which moving away medially is an extended saccus.

Valvae in A. flaviventris Stgr. are elongated, lamellar with sharply reduced intravalvar muscles (m7), which from the inferior angles of valvae lead to crests on sacculi (crista sacculi). These crests, just as the apical parts of valvae, are densely covered by modified sensory chaetae. The superior angles of valvae are transformed into lamellate basal processes, attached to which are muscles m4, implementing the flexor function of valvae. These muscles begin at the apex of the vinculum arches close to their articulation with tegumen. It is not excluded that a part of the muscular fibers get transmitted on tegumen.

7

The additional flexor function of valvae is accomplished by aedeagus protractors (m5), leading from the short basal growth of aedeagus into valvae towards their external wall. The abduction function of valvae in connection with reduction of tergal valvae extensors (m2) is taken on completely by muscles m3, connecting the superior and lateral parts of saccus with juxta. The structure of the juxta and its linkage with muscles m3 are quite unique. The juxta is represented by an extended sclerotized frame, sitting on a transverse sclerite. Muscles m3 are segmented and consist of unpaired medial muscle, which extends to the apex of juxta, and two muscles, leading to lateral angles of the transverse sclerite.

The attachments of muscles activating the aedeagus (m3 and m6) are shown in Fig. 5 B.

Besides A. flaviventris Stgr., one more species from the genus Aegeria F. was partially investigated - A. tripuliformis Cl. The genital skeleton and musculature of this species are the same as in A. flaviventris Stgr.

## Family COSSIDAE

Cossus chinensis Rotsh., Cossinae (Fig. 6 A). This East-Asiatic species of the Holarctic genus Cossus F. is very close to the type species. Sometimes (Daniel, 1954 - 1965) regarded as a subspecies of C. cossus L. From the nature of genital skeleton and musculature this species is principally not different from the majority of other Papilionomorpha. The vinculum is narrow with a bulky saccus. The relatively broad tegumen is articulated with the beak-shaped unpaired uncus, which is activated by depressor muscles m1. With their contraction these muscles depress the uncus, pressing it to the sclerotized gnathos. Between the uncus and gnathos is the anal cone, muscles m10 penetrate into its distal from tegumen part.

The valvae are broad, most of the surface of their internal wall is membranous, with exception of the superior, inferior and proximal edges. The intravalvar muscles (m7) are developed in the inferior region of the valvae (in sacculi).

A peculiarity of the genitalia in C. chinensis Rotsh. is the unusual nature of the basal processes. The superior sclerotized edges of the valvae form strong broad sclerites, passing onto diaphragma and practically locking one with another on the medial line. Muscles m2 and m4 are attached to the superior edge of lamellate basal processes. Moreover, muscles m2 lead from tegumen to superior lateral angles of processes. Contraction of these muscles implements abduction of valvae. Muscles m4 take up sternal position, leading away from vinculum and are attached to basal processes dorsomedially. Contraction of muscles m4 causes abduction of valvae.

Sclerotization of the superior edge of valvae spreads also on the whole of their proximal region, where broad sclerites form, pointed at the end, directly fused with the lamellate basal processes and clearly articulated with the juxta. Implanting into the valvae under these sclerites are the aedeagus protractors (m5).

8

Muscles m3 are well developed and lead from the base of juxta to posterior edge of the medial region of the vinculum, accomplishing with their contraction the abduction of valvae, i.e. serving as synergists of muscles m2. Thus, the valvae shift due to contraction of muscles m4 and m5 and their abduction to the sides is implemented by muscles m2 and m3.

The aedeagus is of relatively primitive structure - there is no basal growth, and the anellus is fused with the tubule of the aedeagus only in its proximal part. In this case the aedeagus retractors (m6) partially enter on anellus. Developed within the aedeagus are the intraedeagal muscles (m21 - m. intraaedoeagalis) typical for Papilionomorpha, described for the first time by Forbes (1939) as protractor-muscles of vesica.

Dyspessa ulula Borkh., Cossinae. Typical species of the Palaearctic genus Dyspessa Hb. From the structure of genitalia, it is similar in many aspects with Cossus chinensis Rotsh. There is the presence of the beak-shaped uncus, provided with muscles m1, of horseshoe-shaped gnathos and broad tegumen, from mediocranial region of which lead two pairs of muscles: to the edges of subanal plate (m10) and to the basal processes of valvae (m2). At the same time in the region of the subanal plate discovery was made of muscles m20, so far found only in Pennisetia hylaeiformis Lasp. It is possible that these muscles are developed in many Lepidoptera, but represent parietal lining of the medial part of anal cone, and their fibers are not grouped into clearly delimited muscles. Practice shows that study of muscles in the anal region deserves greater attention than previously allotted.

Valvae and their musculature in D. ulula Borkh. and C. chinensis Rotsh. bear features of profound similarity, differing only in details. Basal processes of valvae, just as in C. chinensis Rotsh., are modified into broad medially directed sclerites, almost contiguous on middle line. Approaching superior angles of lamellate basal processes are muscles m2 and m4. Muscles m3 bind internal apodemes of juxta with medio-caudal part of vinculum; their contraction, bending the superior part of juxta inside, opens the valvae. Muscles m7 are located within the sacculi of valvae. The positions of aedeagus muscles are also not different from their topography in C. chinensis Rotsh.

Phragmataecia castaneae Hb., Zeuzerinae (Fig. 6B). Bases of the upper edges of the valvae are extended and directed medially, forming basal processes, to which are attached muscles m2 and m4, taking up on the ring of the 9th segment the same position as in C. chinensis Rotsh.

The peculiarity of P. castaneae Hb. is the considerable reduction in degree of development of intravalvar muscles (m7) as well as reduction of gnathos. The attachment of muscles m1, m3, m5, and m6 is the same as in C. chinensis Rotsh.

Zeuzera leuconota Wlkr., Zeuzerinae (Fig. 7). The East Asian vicariant of the type species of genus Zeuzera Latr., distributed almost universally. Morphologically so similar to the European type species of the

genus, Z. pyrina L., that quite possibly it is only its eastern subspecies.

Just as in all species of family Cossidae studied, in Z. leuconota Wlkr., developed in the tergal region of genitalia are the beak-like uncus, horseshoe-shaped gnathos and broad tegumen, leading from which are 3 pairs of muscles; m1 - towards the uncus, m10 - to anal cone, and m2 - to basal processes of valvae. The basal processes are not large and widely spaced one from another, just as in Phragmataecia castaneae Hb. Approaching them are muscles m2 from tegumen and muscles m4 from vinculum.

Within the valvae in sacculi are small intravalvar muscles (m7). Attached to the external wall of valvae, slightly dorsally of the attachment point of muscles m7, are the aedeagus protractors (m5), which not only push out the aedeagus, but implement fixation (m6) binding the middle part of aedeagus with sacculus. Basal growth of aedeagus is not defined.

Morphological analysis of the juxta, located between sacculi of valvae, deserves special attention. Distally the juxta forms 2 processes, which implement no active mechanical function of any kind. The plate of juxta is most heavily sclerotized close to the base of the distal processes, where muscles m3 attach, as well as laterally and in cranial part. Sagittaly the juxta is fixed by the stiff ridge. With contraction of muscles m3, the apex of juxta is slightly pulled into the abdomen and, due to the presence of the stiff ridge, does not bend. Constructive rigidity of juxta enables it to make a mechanical lowering into the lower part of the abdomen when its tip is retracted into the abdomen. This pressure is directed here backward and upward, which thereby ensures the abduction of the valvae to the sides. This type of juxtal functioning is typical for the majority of Papilionomorpha. However, the second peculiarity of the Z. leuconota Wlkr. juxta is the presence of muscles m13 (m. juxta-sacculalis). These muscles are represented by several weak fibers, leading from the lateral part of juxta to the base of sacculi. Simultaneous presence of muscles m3 with muscles m13 in Z. leuconota Wlkr. emphasizes the profound archaity of the family Cossidae as a whole.

Birket-Smith (1974a, 1974b) has recently investigated 2 species from the widely distributed tropical genus Xyleutes Hb. (Zeuzerinae) occurring in Australia, New Guinea and South Africa - X. biatra Hampson and X. crassus Dr. Comparison of morphological data obtained from Palaearctic species of Cossidae compared with detailed descriptions of the skeleton and musculature and genitalia in species studied by Birket-Smith, has shown a high similarity in functional organization of Zeuzerinae taken from various zoogeographical regions. Nevertheless, Birket-Smith described in X. biatra Hmps. besides the muscles leading from juxta, m3 and m13 (his m8 and m10 respectively), another 2 pairs of muscles. Birket-Smith described muscles m9, most probably the result of separation of muscles m3 (m8 of Birket-Smith), and muscles m11, located entirely within the juxta and not found in Palaearctic Zeuzerinae, are also obviously, the result of juxta musculature differentiation.

10

## Family LIMACODIDAE

Monema falvescens Wlkr. (Fig. 8) - Type species of the genus Monema Wlkr., distributed in Southeast Asia from Japan to the Himalayas. In comparison with other species of the family investigated, in M. flavescens Wlkr. the genitalia are the least derived and show a number of primitive characters. Opposed to broad uncus is a broad gnathos, uncus depressors (m1) are well developed. The valvae are sharply differentiated into sacculus and cucullus, but the basal processes of valvae are not joined one with another and do not form a transtilla. Approaching these processes are the valvae flexors (m4). The valvar muscles (m7) are strongly developed. Aedeagus protractors (m5) penetrate quite deeply within the valvae. However, in this most primitive of investigated species muscles m2 are already absent and the aedeagus is functionally asymmetrical: the seminal duct enters into it from the side, and muscles m5 are slightly twisted - muscle, leading from the basal growth on the right, passes under aedeagus onto left side of genitalia, and the left muscle above the aedeagus passes onto the right side.

Latoia sinica Moore (Fig. 1 A, B) and Narosoideus flavidorsalis Stgr. - Species of tropical Oriental genera, just as the species of genera distributed in the Northern Hemisphere, Cochlidion limacodes Hufn. (Fig. 9 C, D) and Apoda dentata Obth., have similar genital structure. Retaining the unpaired uncus, gnathos and muscles m1, the lamellate valvae are bound one with another to a different degree by a developed transtilla, emerged on basis of developed basal processes. Leading to transtilla from vinculum are the valvae flexors (m4), and their antagonists (muscles m2) are reduced. Functional asymmetry of the aedeagus reaches the highest degree: the seminal duct enters into it from underneath. Correspondingly, muscles m5, leading from the basal growth, are twisted. Muscle, fixed to the basal growth on the right, passes above aedeagus, going further to the left valvae, and the left muscle under aedeagus passes over to the right side, implanting into the valvae.

## Family ZYGAENIDAE

Zygaena filipendulae L., Zygaeninae (Fig. 10), type species of the widely distributed Palaearctic genus Zygaena F., which contains about 100 species (Burgeff, 1926). The 9th segment in this species is quite well developed, moreover, the tegumen is clearly articulated with vinculum. The uncus is paired, and muscles m1 are attached each to its own part of paired uncus. The valvae are broad, oval, with small basal processes, to which muscles m2 and m4 approach from tegumen and vinculum. The internal walls of the valvae are bound at the base with one another by means of a complicated differentiated anellus, through which the aedeagus passes. In this case muscles m6 shift from aedeagus to anellus, and m5 takes up the archaic position, binding the basal projection of aedeagus with the external valvae walls. Muscles m3 lead from juxta to the membrane above the caudal part of the medial region of vinculum. Intravalvar muscles (m7) are not present.

11

Balataea octomaculata Brem., Procrinae (Fig. 11). The only species known in the USSR fauna and type species of the genus Balataea Wlkr., distributed in Eastern and Southern Asia. About 20 species are included in this genus. Balataea Wlkr. is included in the tribe Procrini, but differs sharply in structure from the type genus of this tribe.

In the appearance of a butterfly, B. octomaculata Brem. shows a clearly defined similarity with clearwing moths (Sesia apiformis Cl.) and could be an example of Lepidoptera mimicry, the model for which were some Hymenoptera. In contrast to Zygaena filipendulae L., the uncus in B. octomaculata Brem. is unpaired, but the median suture is clearly traced on it. Moreover, the intravalvar muscles (m7) are present. The most substantial difference is shape and structure of the transtilla, which was formed as a result of sclerotization of the upper part of anellus, which binds the valvae. Transtilla muscles m2 emerged in this way approach from tegumen, m4 from vinculum and m5 from aedeagus, moreover, the latter pair of muscles is attached on boundary of the transtilla transition into valvae. The other peculiarity of this species genitalia is the transition of muscles m3 onto sacculi of valvae. Thus, in B. octomaculata Brem. an even higher degree of specialization is observed than in Z. filipendulae L.

Illiberis pruni Dyar, Agalopinae (Fig. 12). Determined from the work of Alberti (1955). Typical species of a small East Asian subgenus Primilliberis Alberti. Defined in this subgenus in comparison with previously analyzed specimens of Zygaenidae was the following stage of specialization of genitalia. Transtilla extremely hypertrophic, and formed on it is a gnathos-like appendage. Moreover, the valvae and transtilla fuse with the lateral parts of tegumen, i.e. emerge extremely unusual morphological deviations, which also effects the musculature. Thus, muscles m2 approach from above to the internal apodemes of transtilla but not from tegumen, as in other Lepidoptera, but from the base of uncus, where these muscles are attached jointly with muscles m1. The second pair of muscles in other species analyzed being attached on vinculum. These muscles approach the inner apodemes of the transtilla from underneath.

High specialization of I. pruni Dyar is also manifested in position of aedeagus protractors (m5), which are attached to the base of transtilla, and in reduction of intravalvar muscles m7.

The uncus is unpaired and, just as in A.-octomaculata Brem., divided by a primary median suture.

In spite of such profound specialization of genitalia in I. pruni Dyar, muscles m3 are not as yet completely passed onto sacculi of valvae and part of their fibers are attached to vinculum. Moreover, the aedeagus is, apparently, primarily deprived of basal projection. Intraaedeagal muscles (m21) are present.

Elcysma westwoodi Snell., Agalopinae (Fig. 13). Type species of monotypic, Eastern and Southern Asia genus Elcysma Butler. This species is represented in the USSR by subspecies E. westwoodi caudata Brem., which was the one we studied. Defined in it was a further stage of specialization of genital structures. Transtilla

fuses with lateral edges of tegumen already at a considerable distance, and its gnathos-like medial projection, just as in I. pruni Dyar, is formed directly under the anal tubule. Exactly in the same way approaching the inner apodemes of transtilla are two pairs of muscles m2 and m4. Muscles m4 lead from vinculum, and m2 from subanal plate. Thus, if in B. octomaculata Brem. muscles m5 lead to transtilla from tegumen, in I. pruni Dyar these muscles approach apodemes of transtilla from the base of uncus, and in E. westwoodi Snell. muscles m2 lead to the same apodemes already from subanal plate. The aedeagus protractors (m5) shift considerably higher and are attached to medial projection of transtilla.

Muscles m3 are divided into two pairs, one of which (m3a) leads from juxta to sacculi of valvae, attaching to the wall separating adjacent one to another bases of valvae. Muscles m3b lead directly from sacculi and get attached close to the juxta at the transtilla base.

The aedeagus, just as in I. pruni Dyar, is devoid of a basal process. Even in Balataea octomaculata Brem., considerable constriction of tegumen is noted; in I. pruni Dyar area reduction of the 9th dorsal region of tegumen disappears, and the anterior wall of genital ring forms from above the base of a broad uncus with a bifurcated end.

Intravalvar muscles (m7) are reduced.

Pryeria sinica Moore, Zygaeninae, Pryerini. Type species of the monotypic East Asian genus Pryeria Moore. Its genitalia have evolved in a different direction. In this species there is no emergence of transtilla, and the basal processes are also absent. Valvar muscles are attached directly to the base of superior edge of the valvae, moreover only one pair is developed (m4). Muscles m2 are reduced. The peculiarity of P. sinica Moore is transition of attachment point of aedeagus protractors (m5) from valvae on vinculum. As a result of this shifting of m5 and reduction of intravalvar muscles (m7), the only muscles implementing flexor function of valvae become muscles m4. This in turn, caused their strong development. Just as highly developed are muscles m3, the only muscles abducting valvae to the sides. Leading from juxta, they are attached both to vinculum and sacculi of valvae.

The uncus retains paired structure and is equipped with depressors (m1).

Aedeagus with basal growth. Muscles m21 are well-developed within the aedeagus.

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POSITION OF SUPERFAMILIES SESIOIDEA, COSSOIDEA, AND

ZYGAENOIDEA WITHIN THE SYSTEMATICS OF THE PAPILIONOMORPHA

Representatives of most of the subfamilies and tribes of the Choreutidae, Sesiidae, Cossidae, Limacodidae, and Zygaenidae are found in the (Soviet) Far East. Therefore study of the Eastern Asiatic representatives of these families will provide significant material for an explanation of the phylogenetic

13

relationships of the mentioned taxa and their position in the infraorder Papilionomorpha.

In most of the systematic work on these groups they have been widely separated and such a tendency has persisted into the present. Nearly every worker has had his own idea concerning their position in the system.

A.M. Gerasimov (1948) and J. Heppner (1977) have found the greatest closeness of relationship in these groups. Gerasimov separated a series of families of the Zygaenoidea (Zygaenidae, Limacodidae) and Tortricoidea (Sesiidae, Cossidae, Tortricidae) only as the series Tineoidea, but he did not remove a series of genera close to Choreutis Hbn. from the Glyphipterigidae. Heppner set up a series of superfamilies - Sesioidea (Immidae, Sesiidae, Choreutidae), Tortricoidea, and Cossoidea - but placed them far from the Zygaenoidea.

In one of the most thorough and morphologically well-founded evolutionary schemes of the world fauna of Lepidoptera, Brock (1971) included the 5 families here treated along with a few other groups in 3 superfamilies:  Cossoidea (Cossidae, Ratardidae, Metarbelidae, Dalceridae, Megalopygidae, Limacodidae, and Chrysopolomidae), Sesioidea (Sesiidae, Choreutidae), and Zygaenoidea (Zygaenidae).  In so doing he considered these 3 superfamilies to have evolved radially from a common ancestor.

A functional-morphological and comparative analysis of the skeleton and musculature of the male genitalia in the 5 studied families has disclosed some characters common to the Papilionomorpha in a plesiomorphic state:  basal processes present on valvae; the system of uncus, gnathos, and lamellar juxta; presence of 11 pairs of genitalic muscles (m1-m7, m10, m13, m20, m21); sternal position of m4; removal of m3 from vinculum; introduction of m5 into the valvae; etc.  Therefore, even if no reliable criterion for uniting these groups into one monophyletic taxon was found, it may be noted that a primitive morphological basis was found in the most archaic subfamilies or tribes of the studied families.

A few families or subfamilies, however, are characterized by characters in an apomorphic state: functional asymmetry of the aedeagus; modification of the uncus and socii, loss of gnathos, reduction of m2 or m7; etc.  This permits their being reconsidered or more precisely defined as to their position within the infraorder.

### Superfamily SESIOIDEA

In the recently published evolutionary scheme (Heppner, 1977), this superfamily was placed between Yponomeutoidea and Tortricoidea.  Phylogenetic proximity of Sesioidea and Tortricoidea has been noted in the structure of larvae (Gerasimov, 1952), pupae (Mosher, 1916) and adults (Brock, 1971), however, functional-morphological analysis of male genitalia has not produced new characters indicating close relation of these superfamilies.

It may be mentioned that the most primitive of the investigated Choreutidae, the genus Anthophila Hw., is similar to Tortricinae in the shape of uncus, gnathos, valvae, and juxta, but this similarity has, possibly,

emerged as a result of parallel evolution. Some characters have also been defined which are expressed in plesiomorphic states in Sesioidea, and apomorphic in Tortricoidea. Thus, intravalvar muscles (m7) are developed in many Sesioidea and are always absent in Tortricoidea (Kuznetsov and Stekol'nikov, 1977); muscles m4 in Sesioidea lead from the vinculum, and but in Tortricoidea from the tegumen. Such peculiarities, indicating phylogenetic advancement of Tortricoidea, also do not exclude distant relation of these superfamilies.

Not pausing on the tropical group Immidae, let us analyze the phylogenetic relations of two other families being included in the superfamily Sesioidea.

Family Choreutidae Wocke, 1871 is widely distributed. Until recently it has been assumed that it is represented most abundantly in tropical countries, but possibly this is not so. A number of large tropical genera were previously included here: Hylarographa Z., Thaumatographa Wlsgm., Mictopsichia Hb. and others were transferred into tribe Chlidanotini of the family Tortricidae (Diakonoff, 1977; Heppner, 1977, 1978; Danilevsky and Kuznetsov, 1979). The extensive genus Imma Wlkr. probably represents an independent family Immidae.

In the Palaearctic, the family Choreutidae is represented by only a few genera, forming a comparatively compact group, which has not been divided by taxonomists into subfamilies.

There is no single opinion regarding the position of Choreutidae in the system of the infraorder. Usually it has been included at the rank of subfamily as Choreutinae (Spuler, 1910; Hering, 1932; Gerasimov, 1948) in Glyphipterigidae, until basic differences were discovered in the nature of articulation of abdomen with thorax (Brock, 1968), subsequently strengthened by no less substantial differences in the structure and function of male genitalia (Kuznetsov and Stekol'nikov, 1976 - 1977). It has been suggested (Brock, 1971) to refer Choreutidae to the superfamily Sesioidea (Aegeriodea), but this has also been rejected (Heppner, 1977) by structural analysis of adults and larvae.

The present morpho-functional investigation has covered all genera of Choreutidae in the USSR fauna, except the monotypic European Millieria Rag. and the East Asian and American Brenthia Clem.

Genitalic comparison of the most archaic Holarctic genus, Anthophila Hw., with genitalia of Sesiidae has detected some common features; these are origin of m4 from the apex of saccus (mentioned also in Sesiinae), insertion of muscles m3 in the intervalvar region (just as in Pennisetia Dehne), considerable development of the aedeagus basal process, transformation of uncus into sensitive lobes (socii) which retain muscles m1, presence of gnathos (developed also in Sesiinae); some of these characters are expressed in apomorphic states in both families. However, their parallel evolution is not excluded. In any case, the development of the gnathos and transition of muscles m4 onto the apex of saccus are undoubtedly the results of parallel evolution. Nevertheless, with the presence in the two groups of profound common archaic features, parallel evolution of apomorphic characters may indicate relation of these groups, although in this case it is impossible to determine

the extent of this relation. Thus, it is possible to support unifying Choreutidae and Sesiidae into one superfamily; however, this does not mean that the indicated families are closely related. In any case, they evolved in different directions.

Clearwing moths (Sesiidae), retaining the latest mode of life and endophagy of morphologically archaic larvae, generalized structure of pupae, are adapted as adults to a diurnal mode of life, having sharply transformed their appearance. Elongation and constriction of wings, and their transparency, emerged as a result of losing scaly integumen, costalization of forewings, bright color of transverse rings on abdominal segments, clavate antennae and other changes resulted in mimicry and amazing similarity of these Lepidoptera with the suborder Aculeata or with some Diptera. The frenulum, which even in females in this group consists of 1 seta, apparently did not fully ensure the similarity of start of flight, and even in the coupling apparatus of Sesiidae an interesting parallelism with Hymenoptera appeared. This apparatus in clearwing moths is specialized in such a way that the dorsal edge of forewing is bent down, and the costal edge of hindwing bent upward, which ensures (with the presence of setae along these edges) coupling of wings at considerable extension.

Choreutidae are also adapted to a diurnal mode of adult life but retain relatively generalized appearance; the usual shape, coupling and venation of wings, usual structure of cirri, abdomen and legs, however this family has specialized immature stages. Larvae, living openly, have acquired a spindle-shaped body and higher mobility, and sometimes quite bright body color. Pupae have lost one row of spines on the majority of abdominal segments. Without the help of functional morphology it would have been difficult in this case to decide which of these families is more advanced, especially because there are some genera in which the characters of these families are combined. In particular, among the Choreutidae is an Australian-South American genus, Sagalassa Wlkr., which in larval characters is indiscernible from the clearwing moths, and the adult wings also have transparent sections (Heppner, 1977).

Analysis of peculiarities of the skeletal-muscular system enables us to conclude that the family Choreutidae, even judging from the most generalized of genera investigated (Anthophila Hw.), is a phylogenetically more advanced group than the clearwing moths, as the males of this genus possess more apomorphic states of functional morphological characters of genital structure than do clearwing moths.

These characters include, first of all, the loss of muscles m3. Moreover, reduction is noted of m20 and clearly defined tendency for reduction of tergal region and oligomerization of valvar muscles - the valvae are activated only by sternal extensors (m3) and muscles m5, which move the valvae with their constriction. In parallel with reduction of muscles m2 and muscles m4, the intravalvar muscles (m7) acquire high functional significance. These muscles, by bending the valvae, participate in holding the female abdomen with the valvae. Moreover, the fixing role of valvae is intensified by development of sclerite structures on their internal

surface and appearance of extensive fields set with strong chaetae.

A morphological series is defined among the Choreutidae, in which distinctly the most archaic male genital structure is <u>Anthophila</u> Hw., which retains uncus, muscles m1 and sternal position of m4. In subsequent evolution (<u>Tebenna</u> Billb., <u>Choreutis</u> Hb., <u>Eutromula</u> Frol.) reduction occurs of the uncus and its muscles with retension of socii, as well as reduction of m4.

Family Sesiidae Boisduval, 1828 has long been isolated at family rank. In the world fauna, the widely distributed family contains over 1000 species and about 180 genera, and due to the economic importance of the larvae of many clearwing moths, this family has been studied at high scientific level during recent years in Europe (Popescu-Gorj et al., 1958; Niculescu, 1964; Roovers, 1964; Fibiger and Kristensen, 1974), in North America (Engelhardt, 1946; MacKay, 1968; Duckworth and Eichlin, 1977; Duckworth and Eichlin, 1978) and Australia (Duckworth and Eichlin, 1974).

Recently Naumann (1971) has published a new system of Holarctic Sesiidae with detailed analysis of phylogenetic relationships between the main subfamilies and tribes. Phylogenetic bonds of these taxa were analyzed by Naumann on the basis of principles and methods of Hennig (1953, 1966). Dividing the family into 2 subfamilies, Tinthiinae and Sesiinae, he regarded them as sister groups and subdivided each into several tribes - the first into tribes Tinthiini and Pennisetiini, and the second into tribes Sesiini, Paranthrenini, Melittiini and Aegeriini. As the basis for phylogenetic relationships between all these taxa Naumann used predominantly characters of structure and wing venation, but for phylogeny of the tribe Sesiini he also used peculiarities of genital apparatus.

Unfortunately it was impossible for us to investigate muscular morphology of the small Holarctic tribe Paranthrenini and American-East-Asian Melittiini, but from the analysis of morpho-functional organization of the 4 investigated genera of clearwing moths, represented by 4 other tribes, most abundant in species, it is possible not only to confirm the expediency of isolating the 2 subfamilies, but also of the majority of the presently defined Holarctic tribes.

Typical for subfamily Tinthiinae (judging from morphology of <u>Pennisetia</u> Dehne and <u>Zenodoxus</u> Grote and Rob.) are a number of retained plesiomorphic character states in the male genital structure, not expressed in Sesiinae; presence and nature of insertion of muscles m2 and m4, presence in Pennisetiini of 2 pairs of muscles in anal region m10 and m20, presence of simple basal process and the usual form and structure of valvae, absence on them of special fields or crests (crista sacculi) with sensory setae, simple structure of socii in those cases, when they are present.

To this may be added simple structure of antennae (absence of penicillum on the last segment), hardly reduced scaly integument of forewings: the transparent fields on them are not large (Pennisetiini) or even

altogether absent (many Tinthiini) - slight costalization of radial branches on forewings, etc.

Plesiomorphic features of male genitalia were found in both tribes of the subfamily Tinthiinae. In Tinthiini these include insertion of muscles m3 to vinculum and penetration of m5 into valvae, and in Pennisetiini presence of 2 pairs of muscles in anal region and of uncus besides the socii.

Characters in apomorphic states were also found in both tribes: in Tinthiini, reduction of socii and development of unpaired uncus; and in Pennisetiini transition of muscles m3 from vinculum onto intervalvar region, its sclerotization, dorsoventral direction of m7, development of long basal process of valvae and the nature of m5 insertion to anellus.

Thus, functional morphology of male genitalia does not allow, in the given case, determination of which of these tribes is more phylogenetically advanced.

However, taking into account structural characters of female genitalia and peculiarities of wing venation, it is possible to accept, as mentioned earlier (Naumann, 1971) that the most archaic tribe is Tinthiini. In all genera of this tribe forewing R4 and R5 are free, the duct of copulative sac in females is straight, in many species of Zenodoxus Grote and Rob. and Tinthia Wlkr. The signa is retained in the copulative sac, and on the forewings 3 branches of medial trunk are retained, whereas in Pennisetiini forewing R4 is on common stem or fused with R5 and only 2 medial veins remain, in copulative sac of females there are no signa, and the sac duct forms a large loop.

In subfamily Sesiinae (judging from morphology of Sesia F. and Aegeria F.) in comparison with Tinthiinae, the male genitalia have developed a large number of characters in apomorphic states. These include shifting of muscles m3 from mediocaudal part of vinculum onto distal part of saccus, reduction of muscles m2 and medial part of uncus with development of socii implementing however, various functions - mechanical in Sesia F. and sensory in Aegeria F.; only one pair of anal muscles (m10) has been retained, a transformation of the basal process of the valvae, and emergence on it of crests or fields with strong sensory setae. Another common apomorphic character for Sesiinae is the presence of the gnathos, although its formation in Aegeria F. and Sesia F. may have evolved independently, as indicated by the unusually different form and structure.

In the subfamily Sesiinae, the tribe Sesiini is undoubtedly the most archaic group, differing by generalization of structure of the male genitalia.

The tegumen here remains in the initial position for Lepidoptera and is articulated with socii, and the gnathos even slightly bifurcated. The juxta still does not have the long lateral processes which are typical for other tribes. The seminal duct enters into the tubule of aedeagus, which has the basal process, although obviously modified by development of lateral lobes, inserted in which are the aedeagus protractors m5 (this process is absent in all 3 other tribes).

18

A number of characters in Sesiini, in comparison with other tribes, are in plesiomorphic states. The valvae are still rectangular and have no highly modified sensory setae, inherent to all the other 3 tribes, and the intravalvar muscles (m7) still are well developed. Muscles m3 originate from saccus in a single fascicle.

All this supports the viewpoint of Naumann (1971) and opposes Sesiini as the sister group to the complex of 3 other Holarctic tribes (Paranthrenini + Melittiini + Aegeriini).

Characters intermediate between Sesiini and Aegeriini are expressed in the tribes Paranthrenini and Melittiini: initial stage of formation of androconial apparatus on socii, appearance on the valvae of sensory setae accumulations, development (in Paranthrenini) of the basal processes of valvae, etc. They also have some apomorphies, setting apart each tribe. Of these for Melittiini, for instance, could be named joining of tegumen and vinculum into a single ring, accumulation of sensory setae at the superior edge of valvae, unusually dense scaly fascicles on posterior tibiae with reduction of anal fascicle, etc.

Therefore, leaving without change the taxonomic rank and intermediate position of these tribes between Sesiini and Aegeriini, it is impossible to contrast Aegeriinae (Synanthedontidae) in subfamily rank to all the other clearwing moths (MacKay, 1968).

Aegeriini, doubtless, represent the most phylogenetically advanced, and morphologically specialized group, in which a number of apomorphies are expressed. Let us mention, besides the maximum transparency of wings, the high modification of valvae, development of the long curved basal process, crest with sensory setae on sacculus (crista sacculi), large sensory fields taking up the major part of valvae, reduction of m7. The splitting of m3 on the saccus should also be regarded as an apomorphic state.

On the whole it may be concluded that comparative morphological analysis of the genital skeletomuscular system supports the classification of Sesiidae, and the scheme of phylogenetic relationships of subfamilies and tribes, suggested by Naumann (1971).

### Superfamily COSSOIDEA

There is no consensus as to the taxonomic content of this superfamily. According to one extreme point of view (Borner, 1939), it consists of the single family Cossidae, and sometimes another family, the Metarbelidae, is added (Common, 1970). At the other extreme (Brock, 1971), the superfamily contains 7 families in 2 groups, one predominantly endophagous (Cossidae, Metarbelidae, and Ratardidae) and the other exophagous (Dalceridae, Megalopygidae, Limacodidae, and Chrysopolomidae).

Inclusion in the Cossoidea of the slug-caterpillars (Limacodidae) and 3 closely related families meets with several objections. Even though the male genitalia of the Limacodidae are very similar to those of the Cossidae, several general characters such as the presence of the uncus-gnathos system, the attachment of muscles m5 to the valvae, muscles m4 and m3 coming off the vinculum, the presence of muscles m7 in the valvae and of

19

m21 in the aedeagus should be considered symplesiomorphies and these characters consequently cannot be taken as the basis for arguing that they belong with this group of Lepidoptera. Other general characters of these families, the presence of the transtilla, similarity in uncal structure and that of the gnathos and valvae, may arise parallelly and independently. Therefore, in male skeleton and musculature as well there is no obstacle to rapprochement of the Cossidae and Limacodidae, but there is no kind of general character in an apomorphic state.

The primitive venation of the hindwings and the reticulate-dotted pattern of the forewings are also preserved in many archaic Papilionomorpha of quite various superfamilies.

A few significant and very sharp morphological differences of the Cossidae from the Limacodidae in the adult, pupal, and larval stages indicate, however, that they took different evolutionary paths.

We note that the Cossidae have a horizontal heart (aortal chamber), while the Limacodidae retain its more primitive vertical position (Hessel, 1969) characteristic of the Zygaenoidea and superfamilies related thereto.

The larvae of the Cossidae are endophages and maintain a hidden mode of life in trunks, branches or roots of trees. They have preserved rudiments of the 2nd thoracic stigmata and the 3-rowed, indistinctly differentiated corona on the abdominal legs, while the Limacodidae live as exposed larvae and are extremely specialized (Gerasimov, 1952).

On the other hand, the pupae of the Cossidae, although they also maintain a series of tergal spinules on the abdominal segments, nevertheless appear apomorphic in comparison with those of the Limacodidae; in the Cossidae the first 2 and following abdominal segments have lost their mobility and the cuticle is thicker and less flexible.

It is clear that all of the differences between the Limacodidae and Cossidae in the skeletal musculature system of the genitalia (reduction of muscles m2, functional asymmetry of the aedeagus, and development of its basal process), as well as larval and pupal structure could easily have arisen as a result of evolution determined in ontogenetic stages in favor of an exposed diurnal mode of life from ancestors far removed from the Cossidae.

All this does not permit the retention of families grouped about the Limacodidae in the Cossoidea, as was proposed by Brock (1971), if the superfamily is intended to be monophyletic.

The superfamily Cossoidea has been found most similar in genitalic structure and articulation of thorax to abdomen in the adult, as well as in larval and pupal structure to the Tortricoidea, Sesioidea, Zygaenoidea, and Castnioidea; therefore the taxon most closely related to the Cossidae is most likely one of these 4 groups. For a solution of the problem a comparative study of the skeletal-musculature system of the genitalia of

20

tropical representatives of these would be most desirable, in as much as the few apomorphies found in the adult Cossidae are costalization of the forewing, loss of ocelli, tendency toward development of transtilla, etc., and these do not explain superfamily phyletic relationships because they appear independently in many groups of Papilionomorpha. It may merely be mentioned that of the 3 superfamilies here treated the Cossoidea preserve the maximally generalized structures in adult, larva, and pupa.

The Cossidae Leach, 1815 are doubtlessly the most archaic group of the superfamily, worldwide in distribution with some hundreds of species. In Palaearctic (Daniel, 1954-1965) there are over 20 genera and 120 species of this family, which is represented here by 2 subfamilies: Cossinae and Zeuzerinae.

The most primitive of genera investigated in both subfamilies, Cossus F., Zeuzera Latr. and Xyleutes Hb., show very similar generalized structure. Uncus vigorous, beakshaped, activated by developed depressors (m1), gnathos developed, tegumen broad. Vinculum medially with hollow sac-like sclerotized saccus. Valvae are broad, with intravalvar muscles (m7) and 2 pairs of valvar muscles in primitive state: m2 originates from tegumen, and m4 from vinculum. Instead to external walls of valvae are m5, which implement abduction of valvae and even their flexing. In Xyleutes Hb. and Zeuzera Latr. they are connected with juxta by muscles m13. Muscles m3 link juxta with vinculum, apparently implementing extensor function. The absence of the aedeagus basal process is also, probably, the primary state of this organ, which moreover, is fused with anellus only on a small segment of its proximal part.

A small cloaca is found in Cossidae females (Dugdale, 1974), a character retained out of Papilionomorpha only in Psychidae and in Sesioidea. Absence of signa in carpenter moths is possibly a primary state.

Comparative analysis of the genital skeletal-muscular system has shown that in Zeuzerinae basal processes of valvae are still comparatively short, but valvar muscles by one pair more, as the sacculi are linked with juxta by rudimentary muscles m13. Although the structure of pupae does not indicate primitiveness of Zeuzerinae, as the Palaearctic specimens have no maxillary palpi retained in Cossidae, still the earliest fossil findings of undoubted Cossidae belong to Zeuzerinae. This pertains to Xyleutites miocenicus Kozh. from the fine grained Miocene shales of Stavropol region (Kozhanchikov, 1957) and other even earlier findings. Genus Xyleutites Kozh. is very similar in forewing venation to Xyleutes Hb. and also a has pushed-out distally, separated radial cell and common stem of veins R3, R4, and R5.

In connection with this it is possible to assume that the subfamily Zeuzerinae originated earlier than Cossinae.

# Superfamily ZYGAENOIDEA

The content of the taxon has been very controversial. In it have been included as little as a single family (Turner, 1947) or as many as 10 (Obenburger, 1964) or even 16 families. Most experienced systematists after Borner (1939) have considered as related and included in the superfamily the Zygaenidae, Heterogynidae, Megalopygidae, and Limacodidae, but a few workers (Zerny and Beyer, 1936) have added the Chrysopolomidae or brought near it the Dalceridae and Cyclotornidae (Watson and Whalley, 1975).

In as much as the latter 3 groups have not been studied by us (they are tropical), we limit ourselves to only a few remarks on the phylogenetic relationships of the Zygaenidae and Limacodidae. These families show common traits of organization.

The Limacodidae and Zygaenidae have evolved along adaptational paths in adult, larval, and pupal stages toward an exposed mode of life which has created in them several common apomorphic morphological changes in comparison with Sesioidea and Cossoidea.

In the larvae, adapting to exposed feeding on leaves, there has been a sharp change in the hook apparatus of the abdominal legs on the way to transforming into suckers (Limacodidae) or replacement by a corona of rows of hooks (Zygaenidae). The larvae of both families have developed a colored integument and pupation has taken to occurring in dense cocoons on plants or in litter.

In the pupae, abdominal tergal spinules on the segments have been lost, so that exit from the firm cocoon has been accomplished by other means than in the Cossoidea and Aegerioidea [sic].

In the adults, to a still greater degree than in the larvae, a complex and brightly colored pattern has developed, some simplifications of forewing venation have occurred, as well as lengthening of the proboscis, especially in the Zygaenidae.

All these specializations have taken place on the long evolutionary path of the Zygaenoidea and their phylogenetic advance in comparison to the Cossoidea and Sesioidea, but they tell little about their genealogy.

However, the male genitalia of the Limacodidae and Zygaenidae reveal structural similarities of the plate like juxta and lack of m13, a general tendency toward transfer of muscle m6 onto the anellus (in _Monema_ and _Zygaena_), and tendency toward formation of a basal valvar process. These specializations are not peculiar to the Cossidae and are not well explained by probable parallelism, inasmuch as evolution of the adults in these families has proceeded in different directions, the Limacodidae having adapted by developing cryptic protective coloration and the Zygaenidae by warning coloration.

There are also some genera (_Pseudopsyche_ Obth., _Caffricola_ Hmps., and _Arctozygaena_ Gaede) which are intermediate in external appearance and genitalic structure between the Limacodidae and the Zygaenidae (Alberti, 1955).

Concerning these there is not a sufficient basis for supporting the opinion of Brock (1971) that the Limacodidae are specialized representatives of the Cossoidea. We concur with most other systematists (Spuler, 1910; Borner, 1939; Gerasimov, 1948; Alberti, 1955; Common, 1975; Watson and Whalley, 1975) in considering the 2 families as phyletically related but not sister groups and retain the Limacodidae in the Zygaenoidea.

A few characters of intermediate nature in the nocturnal Chrysopolomidae indicate a breadth of separation in the phyletic relationships of these families. These permit us to consider the Chrysopolomidae, a family of only about 40 African species, as one intermediate between the Limacodidae and the Zygaenidae. In their external appearance, wing venation, and genitalic structure the Chrysopolomidae are very similar to the Limacodidae, but they differ in lacking a frenulum and gnathos. It is known, however, that the male genitalia of the Chrysopolomidae have interrupted, weakened parts of transtilla, to the oral margin of which muscles (probably m4) are attached, enabling them to move, and, as in the Zygaenidae, the anellus has unpaired dorsal processes (Hering 1937, 1960).

The family Limacodidae Duponchel, 1845 (1844) is predominantly a tropical group including about 400 species, represented in Europe and in the Far East by several genera. The tropical fauna of Limacodidae in Africa alone contains 77 genera (Hering, 1955), grouped into several subfamilies. The 5 Far Eastern genera investigated belong to the subfamily Limacodinae and form a very compact group.

Development of a sclerotized gnathos, juxtaposed to the broad unpaired uncus, is typical for this subfamily. Valvae of simple form, lamellate, linked one with another by developed transtilla, emerged on basis of expanded basal processes. Originating from vinculum to transtilla are the valvae flexors (m4); their antagonists, muscles m2, are reduced. Additional function of activating valvae is implemented by aedeagus muscles (m5), which are inserted to the external walls of valvae. Abduction of valvae to the sides is implemented by muscles m3, which link juxta with medial-caudal part of vinculum.

A remarkable peculiarity of Limacodinae genitalia is the functional asymmetry of the aedeagus. In all species investigated the aedeagus is turned at $90^0$ or even at $180^0$, and the seminal duct enters into it from the side or from underneath. Correspondingly, muscles (m5), originating from basal process of the aedeagus, happen to be twisted. However, from comparison with _Eutromula_ Frol. (Choreutidae) it can be seen that the turn of aedeagus in these groups occurs in different directions - clockwise in Limacodidae and counter-clockwise in Choreutidae. It can be added that asymmetry of the aedeagus is a character of low taxonomic rank, and among the tropical Limacodinae (Fletcher, 1968; Inoue, 1970) there are genera with a symmetric copulative organ.

Thus, the structure of the gnathos, uncus, valvae, transtilla and anellus, differing in Limacodidae from Zygaenidae, could be taken as the plesiomorphic states of these sclerites. Since the reduction of m2 and asymmetry of aedeagus within the infraorder Papilionomorpha emerge repeatedly and occur easily, it is impossible

on the basis of these apomorphic characters to assume Limacodidae to be a younger group than Zygaenidae.

Limacodidae also show a more generalized structure of pupae than Zygaenidae. Limacodidae retain maxillary palpi, and mobility of all abdominal segments up to the 7th inclusive elastic thin cuticle.

A high degree of specialization is attained by the dorsoventrally flattened biting midge-like or slug-like larvae of Limacodidae (Gerasimov, 1952). The abdominal legs are modified suckers, moreover, the primary setae on segments are not noticeable, but there are long, sometimes branching, processes. The spinneret at the end is dilated, so that the silk isolated by it resembles not thread, but tape. The emergence of suckers could be, apparently, linked with adaptation of Limacodidae to feeding on enormous leaves of ligneous plants in humid tropics and subtropics.

The large modification in the structure of Limacodidae larvae indicates the long evolutionary path of Limacodidae. This is confirmed by the close bond with the family Limacodidae of large groups of extremely specialized Diptera. In particular, developing on Limacodidae are all 18 species for which the biology is known from a large genus of bee flies Systropus Wiedemann (Bombyliidae), imitating wasps of the family Sphecidae. This genus, including 130 recent species in the tropical fauna, has been earlier widely distributed in Palaearctic, as fossil remains of its species are known from Baltic amber (Zaitsev, 1977).

Family Zygaenidae Latreille, 1809 is distributed worldwide, but attains maximum morphologic and specific diversity in tropical regions. It includes over 1000 species from 165 genera (Tremewan, 1973) of brightly colored, predominantly diurnal, Lepidoptera with very diverse external appearance and internal structure. The composition of the family is still not quite clearly established, and the rank of some taxa included in it varies according to different taxonomists. It is possible that this family is one of the most morphologically heterogenous in the infraorder.

Due to the unusually bright color of adults and abundance of exotic forms Zygaenidae have been intensively studied by nature lovers since long ago, but, although the first monographs appeared at the start of the last century (Boisduval, 1829), serious development of the family's classification began comparatively recently.

After substantial revision of the world fauna (Alberti, 1955), conducted by evaluation not only of external characters, but also of genital structure, Zygaenidae were divided into 3 phylogenetic trunks; each trunk is represented by a group of subfamilies, and the latter subdivided in some cases into tribes. Altogether Alberti accepted 14 tribes and 7 subfamilies: Zygaeninae, Phaudinae, Charideinae, Chalcosiinae, Anomoeotinae, Himantopterinae and Procridinae. In the Far East Zygaenidae reaches maximum diversity of forms for USSR, but this family is represented here only by 3 subfamilies. We managed to investigate only individual specimens from 5 genera, included by Alberti in the subfamilies Zygaeninae, Chalcosiinae and Procrinae (Procridinae).

24

Evolution of adult and larval stages of Zygaenidae occurred in the direction of adaptation to active life in conditions of bright sunshine. Apparently, the transition to a diurnal mode of adult life occurred independently in different groups of the family, and even in the Palaearctic fauna separate nocturnal forms have been preserved (Elcysma westwoodi Snell.). Bright contrasting coloring of diurnal Zygaenidae adults was apparently formed as protection, as it has been proven that some species of this family are poisonous. For instance, in species of Zygaena F. salts of cyanic acid were found (Watson and Whalley, 1975). It is also not excluded that some genera (Pryeria Moore) have changed their appearance, imitating Hymenoptera.

Spindle-shaped larvae of Zygaenidae with pulled-in heads evolved in different directions than larvae of Limacodidae - in forming on the abdominal legs a complex medial row of hooks, which enabled them to hold onto leaves of leguminous and other small-leaved plants.

Functional morphology analysis of genitalia in the 5 genera of Zygaenidae investigated has shown considerable phylogenetic advancement of the family in comparison with Limacodidae and other groups examined. In male genitalia of Zygaenidae a tendency was noted for modifying the anellus and the formation on its base of a uniquely shaped transtilla, which takes on the function of the gnathos: transition is observed of m3 from vinculum onto sacculi of valvae, and m5 from valvae onto the vinculum or transtilla; in a number of cases m7 and m2 have become reduced. However, all these morpho-functional changes of male genitalia, complicating the copulation process (Hewer, 1934), take place within the family and cannot serve as the basis for phylogenetic conclusions, until additional material is first investigated from all of the tropical groups of Zygaenoidea.

Since genital musculature is not as yet studied in the majority of genera which serve as types for subfamilies and tribes of Zygaenidae, the position in the classification of the family of some genera investigated by us remains disputable or not clear. It is possible to mention the considerable separation of Pryeria Moore from Zygaena F., which supports isolation of the tribe Pryerini, but its inclusion in the subfamily Zygaeninae (Alberti, 1955) is hardly justified.

In the system of Alberti the genera Elcysma Butl. (Chalcosiinae) and Illiberis Wlkr. (Procridinae) are referred not only to different subfamilies, but even to different evolutionary trunks. However both the genera are very similar in a group of important characters in apomorphic states, the skeletal muscular system of male genitalia has typical modification of the secondary transtilla, formed as a result of anellus expansion. On this transtilla appear apophyses, taking on the function of apodemes of the two pairs of muscles: m2 and m4. Caudally directed processes of this transtilla take on the function of gnathos. It is hardly probable that such complex transformations have emerged in parallel. There are more grounds to assume that the similarity of these structures indicates relation of Illiberis Wlkr. and Elcysma Butl.

25

Judging from peculiarities of the genital skeleton, the type genera of the subfamilies Chalcosiinae (Chalcosia Hb.) and Procrinae (Procris F.) do not have such an expanded transtilla, therefore, the genera Elcysma Butl. and Illiberis Wlkr. cannot be referred either to the tribe Chalcosiini, nor to the tribe Procrini, but both of them could be included in the tribe Agalopini. The type genus of the latter tribe, Agalope Wlkr. [sic for Aglaope Latreille; ed.], includes some species (A. glacialis Moore) in which the genital structure expresses all the peculiarities of Illiberis Wlkr. and Elcysma Butl., including also the transformed transtilla. In connection with this, the rank of the taxon could be enhanced to subfamily Agalopinae stat. n. and the genera Illiberis Wlkr. from Procrinae and Elcysma Butl. from Chalcosiini transferred into it.

Additional investigations are required for clarifying phylogenetic relationships of Agalopinae with other subfamilies of Zygaenidae.

CONCLUSIONS

1. Morphological research on the male genitalia of Asiatic representatives of 23 genera of Choreutidae, Sesiidae, Cossidae, Limacodidae, and Zygaenidae has indicated that summation of traits of these families (sternal position of the flexor muscles m4 of the valvae; the sternal extensors of the valvae, m3 coming from the vinculum; the presence of intravalvar muscles m7; etc.) are found only in plesiomorphic states, and that therefore it must be considered that the 5 mentioned families do not form a monophyletic group.

2. The discovery of similarities in the tergal appendages and musculature of the genital apparatus in the Choreutidae and Sesiidae permits their taxa, which have been evolving in different directions, to be joined into the superfamily Sesioidea.

3. In the studied genera of Choreutidae we have noted reduction of m20, oligomerization of the valvar muscles, and strengthening of the functional significance of the intravalvar muscles m7. This family therefore may be considered phylogenetically young and morphologically advanced in comparison to the Sesiidae group.

4. The results obtained from a comparative-morphological analysis basically support Naumann's 1971 system and phylogenetic scheme of subfamilies and tribes of the Sesiidae of the Holarctic fauna. Of a pair of sister subfamilies, the Tinthiinae preserve many characters in a plesiomorphic state: the character of attachment of the extensors and flexors of the valvae (m2 and m4), the presence in the anal region of the subanal muscle m20, the absence of sensory fields and ridges on the valvae, the simple structure of the antennal tips, the weak degree of costalization of veins, and the underdeveloped transparent fields on the forewings. The Tinthiinae therefore are to be considered as the phylogenetically older taxon in comparison with Sesiinae.

5. In male genitalic structure, the younger and more advanced Sesiinae show a series of apomorphic characters: transfer of the sternal extensors of the valvae (m3) to the distal part of the saccus, reduction of the tergal extensors of the valvae (m2), further development of the socii, formation of sensory areas on the valvae, etc.

6. The generalized genitalic structure of the Sesiini permits them to be contracted as a sister group to a complex of the 3 other Holarctic tribes of the subfamily, Paranthrenini + Melittini + Aegeriini.

7. The phylogenetically most recent tribe of the Sesiidae should be considered to be the Aegeriini. In this group the skeletal base is strongly modified, as are also the sensory apparatus and the valvae musculature (rudimentary intravalvar muscles m7, fission of the sternal extensors m3).

8. The Cossidae are doubtlessly the most archaic family of all those studied at this time. Nearly all sclerites of the male genitalia of the family appear generalized, with retention of the m. juxta-sacculalis (m13), incomplete female cloaca, retention of coronary position of the crochets of the abdominal legs and

rudimentary 2nd stigma in the larva.

9. The Zeuzerinae are phylogenetically older than Cossinae, inasmuch as the genitalic apparatus of Zeuzera Latr. and Xyleutes Hb. have one more pair of muscles than in Cossus F. and Dyspessa Hb.

10. In the Zygaenoidea, 2 pairs of muscles are lacking (m20 and m13) and other features of morphological specialization have been noted in the adult, larva, and pupa as compared with the Cossoidea and Sesioidea.

11. On the basis of the transfer of the aedeagal retractor m4 to the anellus, similarity of structure of the juxta, and analysis of the morphology of intermediate taxa, there is support for including the Limacodidae in the Zygaenoidea.

12. In studying 5 Far-Eastern genera of the morphologically compact Limacodinae, these appeared in comparison with the Zygaenidae to have a plesiomorphic condition in the sclerites (uncus, gnathos, valvae, transtilla), while there were apomorphic changes in the functional asymmetry of the aedeagus and loss of tergal extensors of the valvae (m2). Considering the generalized structure of the pupae of the Limacodidae, the slug-caterpillars may be considered a phylogenetically old taxon as compared to the Zygaenidae.

13. The Zygaenidae are very heterogenous in their morphological relationships and the material studied was insufficient to draw conclusions regarding phylogenetic connections between their subfamilies.

14. On the basis of the extremely unusual structure of the transtilla resulting from the growth of the anellus and the great morphofunctional changes in the tergal parts of the genitalia of Elcysma Butl. and Illiberis Wlkr., their inclusion in the tribe Agalopini [sic] is proposed and its rank raised to that of subfamily Agalopinae [sic], stat. nov.

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FIGURE LEGEND

an. k - anal cone, anl - anellus, a. tr - apodeme of transtilla, bas. v - basal growth of aedeagus, bas. o-basal process of valvae, vnk - vinculum, v.tr - projection of transtilla, vlv -valva, g - harpa, gnat - gnathos, krn - cornutum, mvlv -intervalvar sclerotized region, sacc - saccus, skl - sacculus, s.pl - subanal plate, teg. - tegumen, tr. - transtilla, unk - uncus, ed - aed, yuks - juxta.

m1 - m7, m10, m13, m20-m21 muscles: m1 - m. unco-tegminalis, m2 - m. tegmino-valvalis superior, m3, m3a - m. vinculo-juxtalis [???] m. juxto-valvalis, m3b - m. sacculo-transtillalis, m4 - m. tegmino-valvalis inferior, m5 - m. valvo-aedeagalis, m6 - m. sacco-aedoeagalis, m7 - m. intravalalis, m10 - m. tegmino-subanalis, m13 - m. juxto-sacculalis, m20 - m. subanalis, m21 - m. intraaedeagalis.

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Fig. 1:  Skeleton and musculature of male genitalia in Choreutidae.

A-Anthophila fabriciana L. Genitalia, ventral view; aedeagus removed.

B-A. fabriciana L. Aedeagus and its musculature, lateral view.

C-Eutromula montana Danil. Genitalia, lateral view.

Fig. 2: Skeleton and musculature of male genitalia in Choreutidae, lateral view.

A-Choreutis ultimana Krul.

B-Tebenna caucasica Danil.

Fig. 3: Skeleton and musculature of male genitalia in Sesiidae, lateral view.

A-Pennisetia hylaeiformis Lasp. Genitalia, aedeagus removed.

B-P. hylaeiformis Lasp. Aedeagus and its musculature.

C-Zenodoxus editha Butl. Genitalia, aedeagus removed.

D-Z. editha Butl. Aedeagus and its musculature.

Fig. 4: Skeleton and musculature of male genitalia in Sesia apiformis Cl. (Sesiidae), lateral view.

A-Genitalia, aedeagus removed.

B-Aedeagus and its musculature.

Fig. 5: Skeleton and musculature of male genitalia in Aegeria flaviventris Stgr.

A-Genitalia, lateral view; aedeagus removed.

B-Aedeagus and its musculature, lateral view.

C-Juxta and its musculature, lateral view.

34

Fig. 6: Skeleton and musculature of male genitalia in Cossidae, lateral view.

A-Cossus chinensis Rotsch.

B-Phragmataecia castaneae Hb.

Fig. 7: Skeleton and musculature of male genitalia in Zeuzera leuconota Wlkr. (Cossidae).

A-Genitalia, ventral view; aedeagus and left valvae removed.

B-Aedeagus and its musculature, lateral view.

Fig. 8: Skeleton and musculature of male genitalia in Monema flavescens Wlkr. (Limacodidae).

A-Genitalia, lateral view; distal part of left valva and aedeagus removed.

B-Aedeagus and its musculature, lateral view.

Fig. 9: Skeleton and musculature of male genitalia in Limacodidae.

A-Latoia sinica Moore.  Genitalia, ventral view, aedeagus removed.

B-L. sinica Moore. Aedeagus and its musculature, lateral view.

C-Cochlidion limacodes Hufn., Genitalia, ventral view, aedeagus removed.

D-Cochlidion limacodes Hufn., Aedeagus and its musculature, lateral view.

Fig. 10: Skeleton and musculature of male genitalia in Zygaena filipendulae L. (Zygaenidae), lateral view.

A-Genitalia, aedeagus removed.

B-Aedeagus with anellus and juxta and their musculature.

Fig. 11: Skeleton and musculature of male genitalia in Balataea octomaculata Brem. (Zygaenidae).

A-Genitalia, ventral view; left part of vinculum, left valva and aedeagus removed.

B-Aedeagus and its musculature, lateral view.

Fig. 12: Skeleton and musculature of male genitalia in Illiberis pruni Dyar (Zygaenidae).

A-Genitalia, ventral view; aedeagus, left part of vinculum and left valva removed.

B-Uncus and transtilla with musculature, lateral view; valvae except the upper cranial

angle abjuncted.

Fig.    13:    Musculature and skeleton of male genitalia in Elcysma westwoodi subsp. caudata Brem.

(Zygaenidae).

A-Genitalia, lateral view; aedeagus and left valva removed, Muscles m2 and m4 on the

right cut, muscles m5 cut off; removed on the right is the proximal branch of the

muscle, on the left the distal; muscles m3 are not shown.

B-Uncus, tegumen and transtilla with muscles, lateral view; muscles m1, m4, and m5
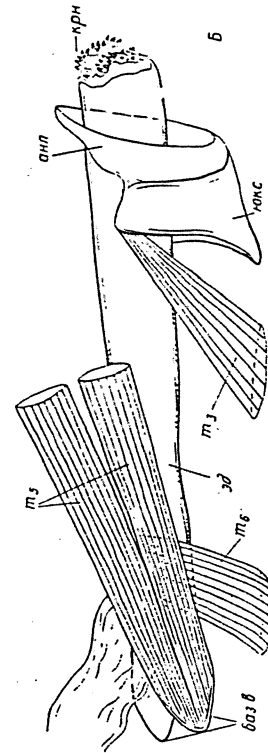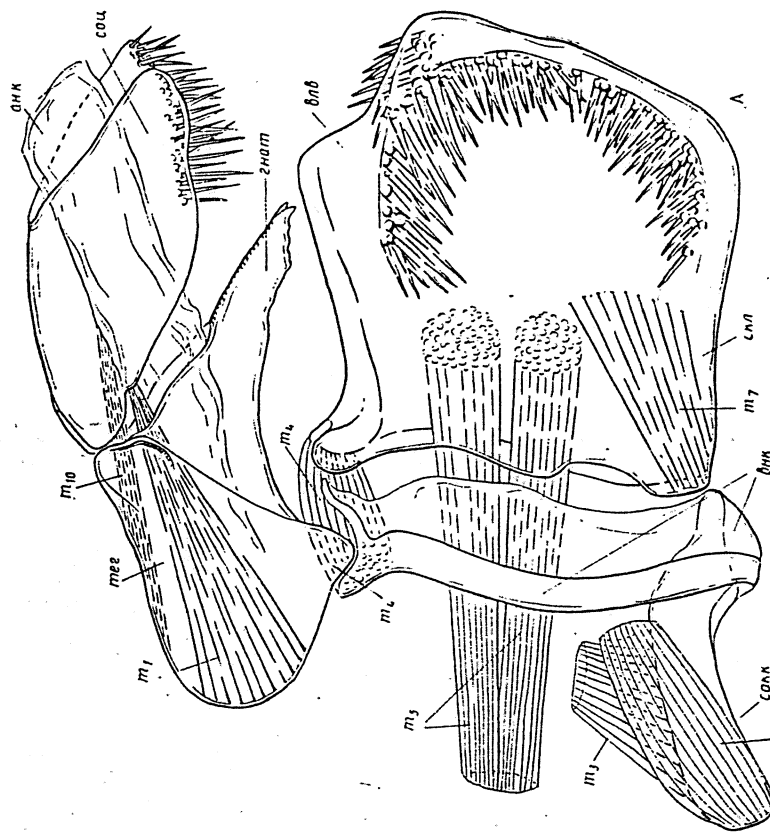
crosscut.

35

Рис. 2. Скелет и мускулатура гениталий самцов у *Choreutidae*, вид сбоку.
*А* — *Choreutis ultimana* Krul. *Б* — *Tebenna caucasica* Danil.

Рис. 1. Скелет и мускулатура гениталий самцов у *Choreutidae*.
*А* — *Anthophila lubricana* L. Гениталии, вид сзади; эдеагус удален. *Б* — *A. lubricana* L. Эдеагус
и его мускулатура, вид сбоку. *В* — *Eutromula montana* Danil. Гениталии, вид сбоку.

Рис. 4. Скелет и мускулатура гениталий самцов Sesia apiformis Cl. (Sesiidae), вид сбоку.

*А* — гениталии, эдеагус удален, *Б* — эдеагус и его мускулатура.
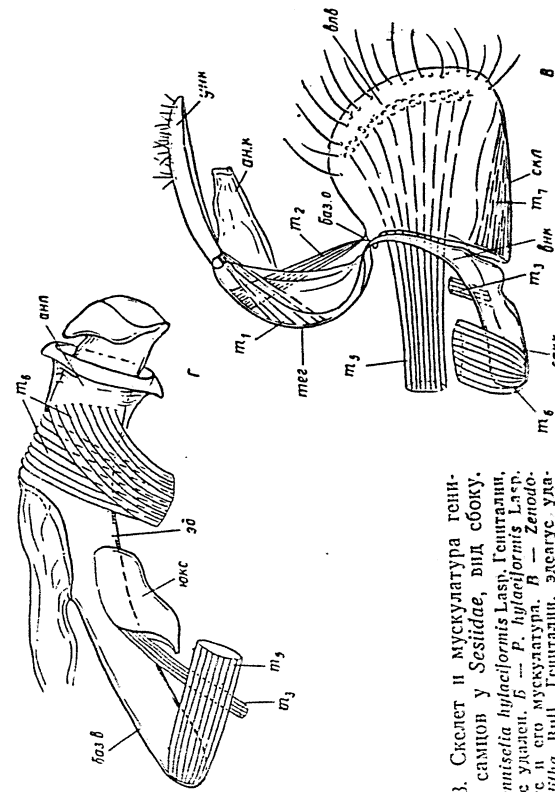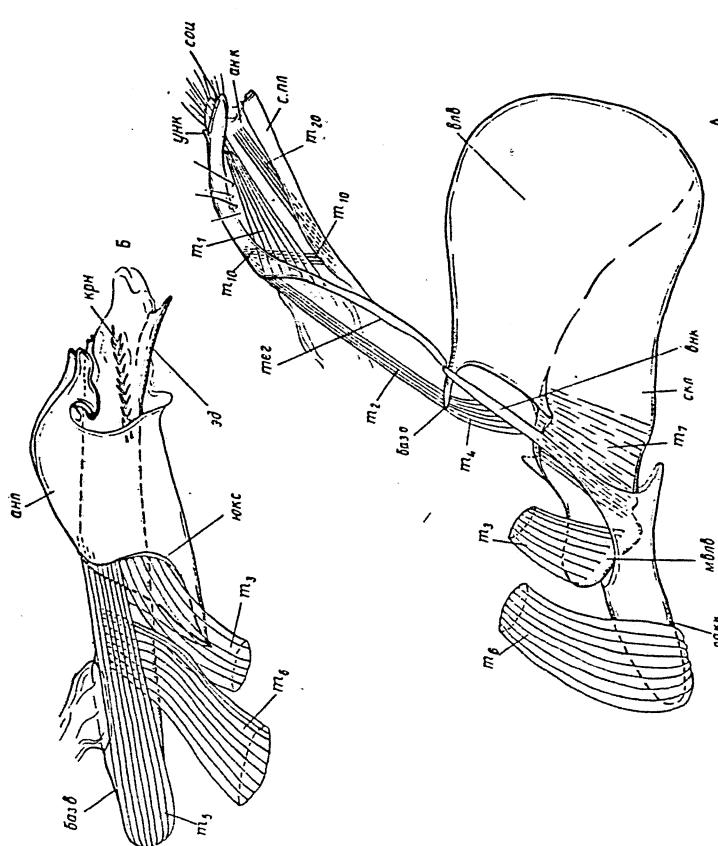


Рис. 3. Скелет и мускулатура гениталий самцов у Sesiidae, вид сбоку.

*А* — Pennisetia hylaeiformis* Lasp. Гениталии, эдеагус удален. *Б* — *P. hylaeiformis* Lasp. Эдеагус и его мускулатура. *В* — *Zenodoxus cithna* Butl. Гениталии, эдеагус удален. *Г* — эдеагус и его мускулатура.

Рис. 6. Скелет и мускулатура гениталий самцов у *Cossidae*, вид сбоку.
*А — Cossus chinensis* Rotsh.; *Б — Phragmataecia castaneae* Hb.
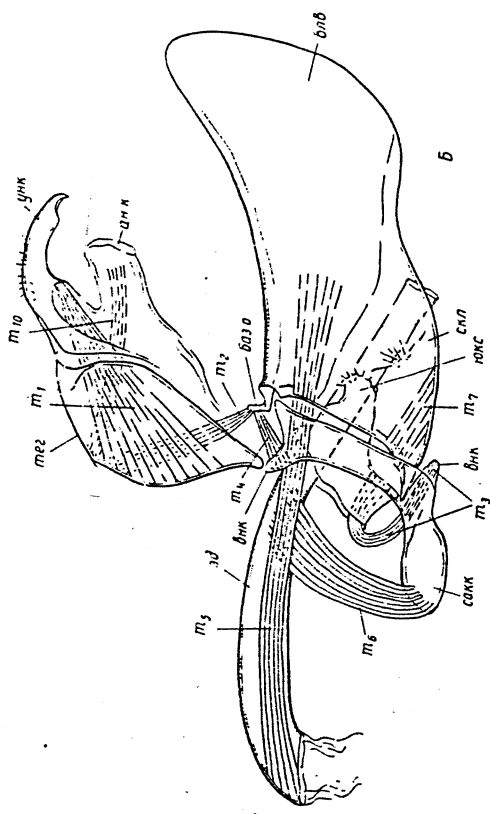


Рис. 5. Скелет и мускулатура гениталий самцов *Aegeria flaviventris* Stgr.
*А* — гениталии, вид сбоку; эдеагус удален. *Б* — эдеагус и его мускулатура, вид сбоку.
*В* — юкста и ее мускулатура, вид сверху.
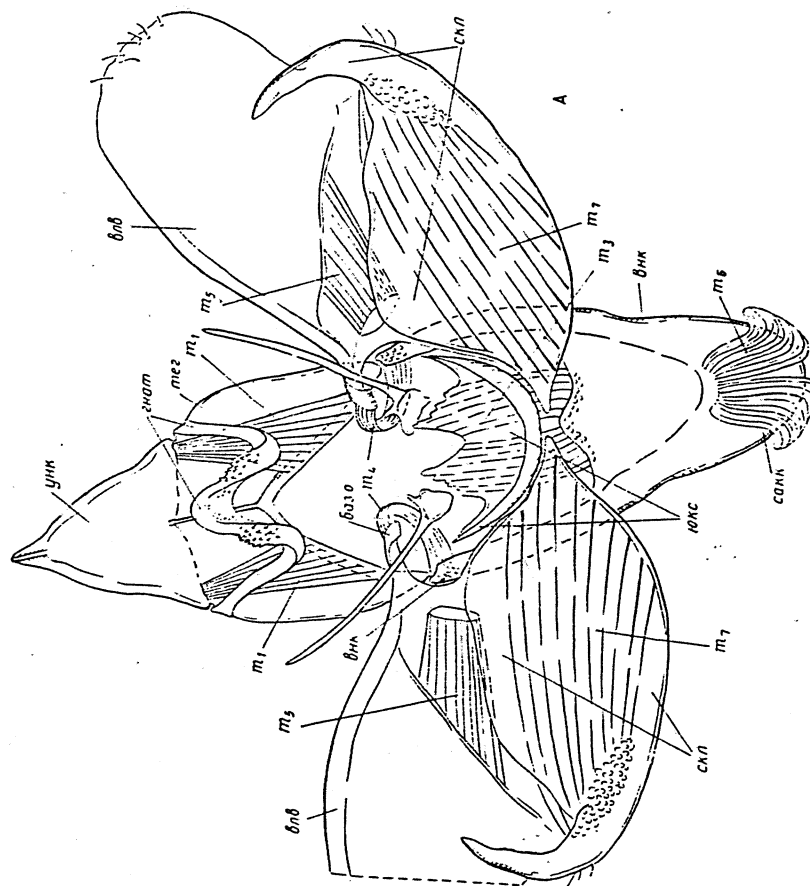
Рис. 8. Скелет и мускулатура гениталий самцов *Monema flavescens* Wlkr. (*Limacodidae*).

*А* — гениталии, вид сзади; дистальная часть левой вальвы и эдеагус удалены. *Б* — эдеагус и его мускулатура, вид сбоку.
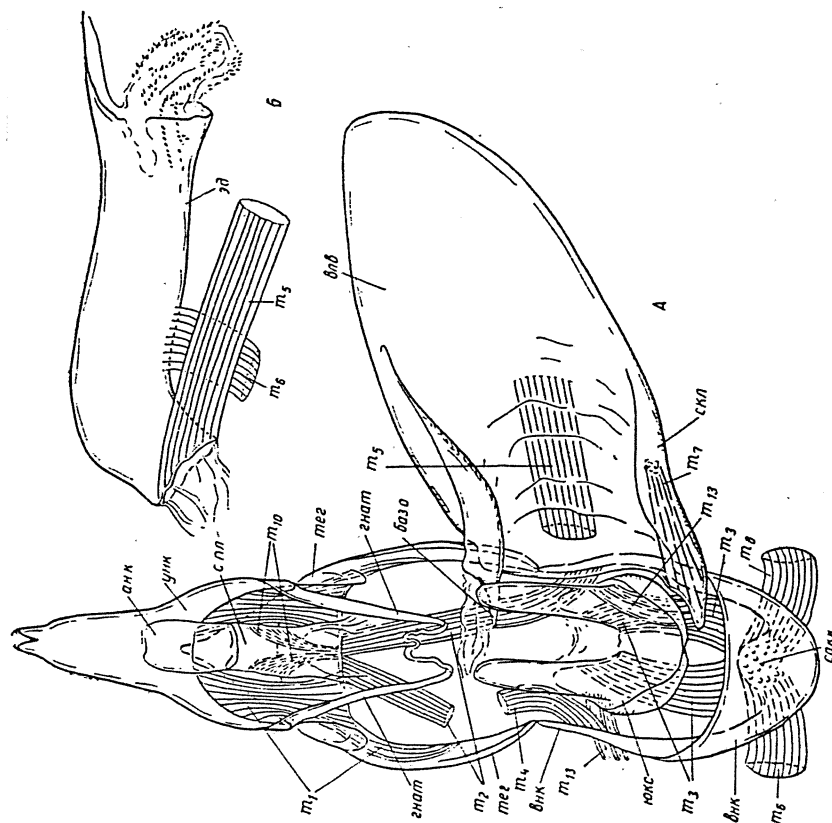


Рис. 7. Скелет и мускулатура гениталий самцов *Zeuzera leuconota* Wlkr. (*Cossidae*).

*А* — гениталии, вид сзади; эдеагус и левая вальва удалены. *Б* — эдеагус и его мускулатура, вид сбоку.

Рис. 10. Скелет и мускулатура гениталий самцов Zygaena filipendulae L. (Zygaenidae), вид сбоку.

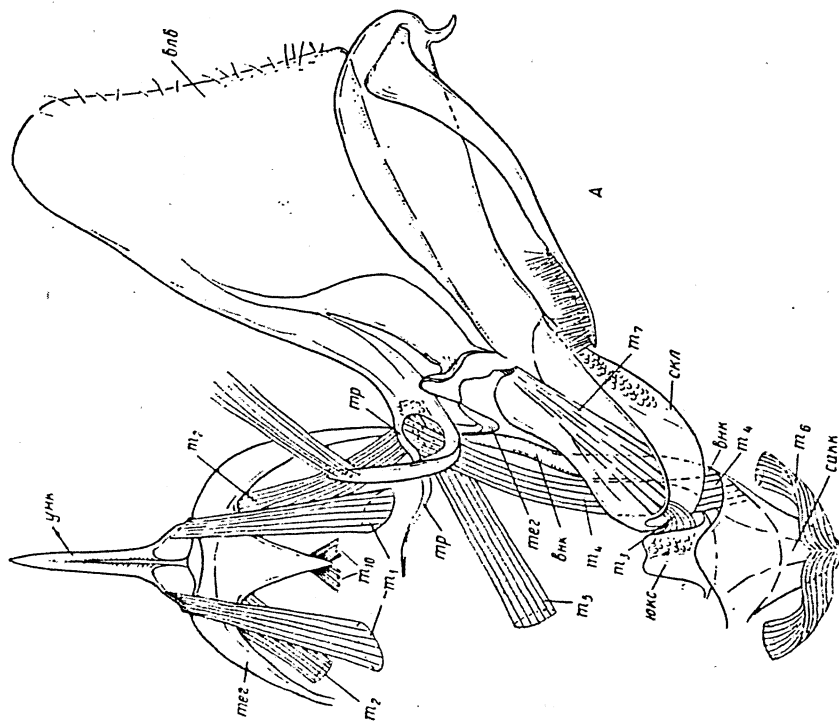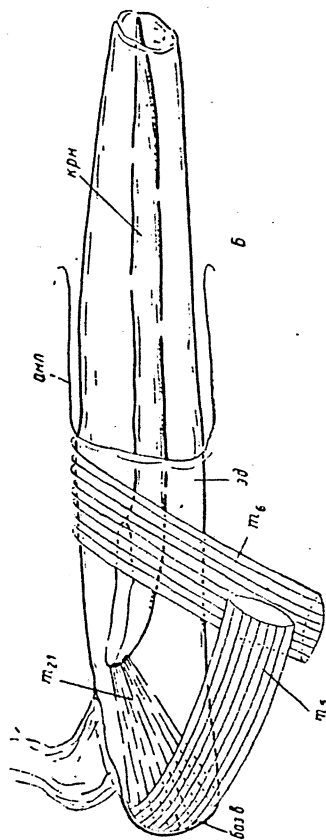A — гениталии, эдеагус удален, Б — эдеагус с анеллусом и юкстой и их мускулатура.



Рис. 9. Скелет и мускулатура гениталий самцов у Limacodidae.

А — Latoia sinica Moore. Гениталии, вид сзади, эдеагус удален. Б — L. sinica Moore. Эдеагус и его мускулатура, вид сбоку. В — Cochlidion limacodes Hufn. Гениталии, вид сзади, эдеагус удален. Г — Cochlidion limacodes Hufn. Эдеагус и его мускулатура, вид сбоку.
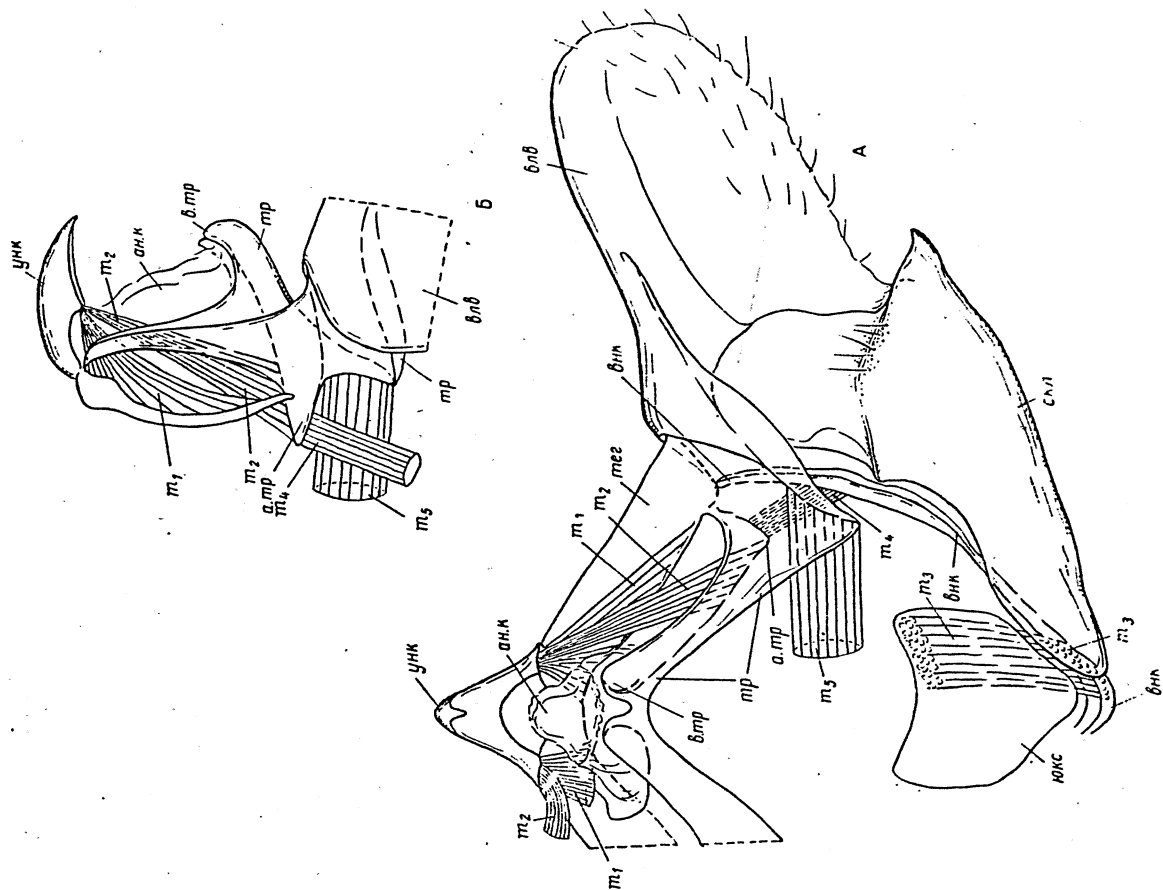
Рис. 12. Скелет и мускулатура гениталий самцов *Illiberis pruni* Dyar (*Zygaenidae*).

*А* — гениталии, вид сзади; эдеагус, левая часть винкулума и левая вальва удалены. *Б* — ункус и транстилла с мускулатурой, вид сбоку. Вальвы, за исключением верхнего краниального угла, отчленены.



Рис. 11. Скелет и мускулатура гениталий самцов *Balataea octomaculata* Brem. (*Zygaenidae*).

*А* — гениталии, вид сзади; левая часть винкулума, левая вальва и эдеагус удалены. *Б* — эдеагус и его мускулатура, вид сбоку.
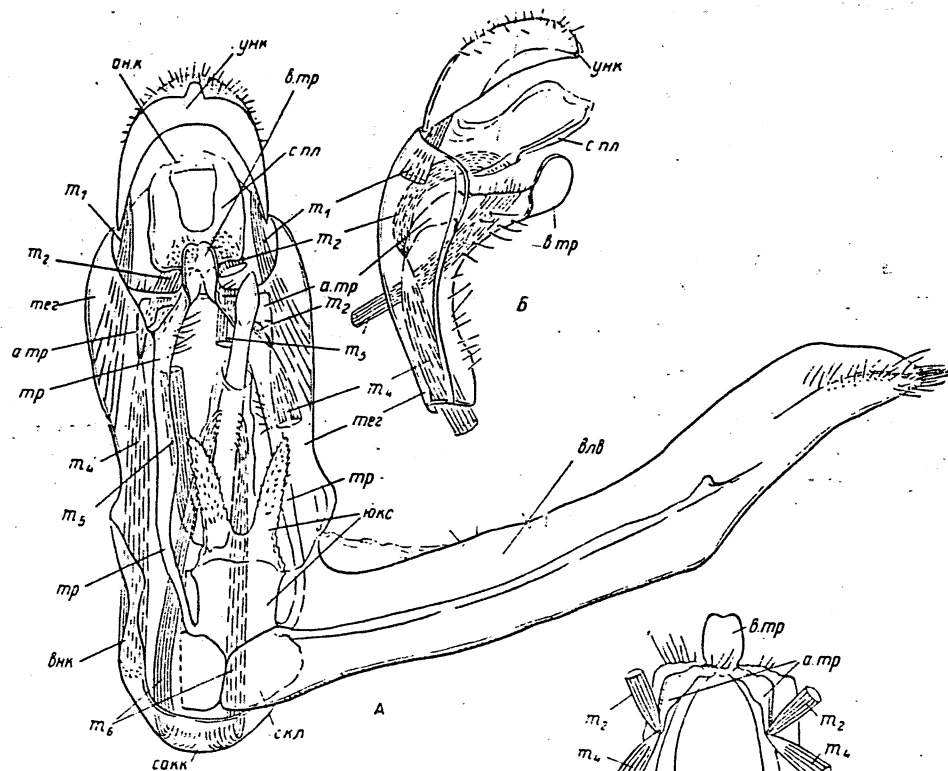
Рис. 13. Скелет и мускулатура гениталий самцов *Elcysma westwoodi* subsp. *caudata* Brem. (*Zygaenidae*).

*A* — гениталии, вид сзади; эдеагус и левая вальва удалены. Мышцы $m_2$ и $m_4$ справа перерезаны, мышцы $m_5$ обрезаны: справа удалена проксимальная часть мускула, слева — дистальная; мышцы $m_3$ не изображены. *Б* — ункус, тегумен и транстилла с мышцами, вид сбоку. Мышцы $m_1$, $m_4$ и $m_5$ перерезаны. *В* — юкста, транстилла и основания вальв с мускулатурой, внутренняя сторона. Мышцы $m_2$ и $m_4$ перерезаны.