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Abstract. The external morphology of the thorax and abdomen of four species of Neotropical Hesperiidae, belonging to different tribes, are described and illustrated. The morphological characters traditionally used in the classification of the family are reviewed and new information is added with emphasis on the characters usually neglected in the classification and identification of Hesperiidae and Lepidoptera. The use of these characters, along with those commonly used in literature for the identification and taxonomy of the family, is discussed, aiming to contribute to comparative studies of morphology and taxonomy of this group.

Key Words. Anatomy, Neotropical, butterflies, skippers.

Resumo. A morfologia externa do tórax e abdômen de quatro espécies de Hesperiidae neotropicais, pertencentes a diferentes tribos na família são ilustradas e descritas. Os caracteres morfológicos tradicionalmente utilizados na classificação da família foram revistos e novas informações são acrescentadas enfatizando os caracteres usualmente negligenciados na classificação e identificação de Hesperiidae e Lepidoptera. O uso destes caracteres é discutido quanto à sua potencial utilidade na identificação e taxonomia da família, além dos comumente utilizados na literatura, objetivando contribuir para estudos de morfologia comparativa e taxonomia do grupo.

Palavras Chave. Anatomia, Neotropical, borboletas, hesperídios.

Introduction

Due to the difficulties in visualizing and understanding thoracic and abdominal sclerites, a great part of the external morphology of the Lepidoptera is not used in the classification systems of the group, or even in phylogenetic studies (Kristensen 1976; Brock 1971; Ackery 1984; De Jong et al. 1996). The majority of the characters used to date are based on the appendages, e.g. wings, legs and genitalia (Watson 1893; Evans 1951-1952; Mielke 2001; Warren et al. 2009).

However, it is highly improbable that there is no useful information in these tagma which can be of great value in Lepidoptera systematics. In the thorax, for example, some of the sclerites have been used to diagnose some families, as well as in the classification of Lepidoptera in general. Niculescu (1978) used the presence and the development of the anepisternum (mentioned as paraesternum) to propose the division of Lepidoptera into two suborders, in general characterizing a strong reduction of the sclerites in butterflies (Papilionoidea). According to him, Hesperiidae present characters from the two suborders, comprising an intermediate group between butterflies and skippers, even though the author classified them as butterflies.

The abdomen presents a similar scenario. Although the genitalia characters are widely used in the description and diagnosis of the species or higher groups (Niculescu 1970), other abdominal structures are only seldom mentioned or, when indicated, refer to the presence or absence of sensitive organs or specialized glands (Barth 1960; De Jong 1972). Ackery et al. (1999) and Mielke (2001) demonstrated that some abdominal tergites might provide strong synapomorphic signs, such as the shape of the first tergum, which diagnoses the Pyrrhopyginae. Furthermore, the large variation of structures which comprise the genitalia, when mentioned by researchers in several taxa, has culminated in an excess of synonymic or homonymic terms that cause confusion during the interpretation of the structures associated to the genitalia (Sorensen, 1980). As early as 1942, Beirne had already accounted for an average of six different names associated to a single structure, while Niculescu (1970) had listed over 900 terms related to genitalia. Even today, the more common terms used taxonomically lack homology criteria (see Michener

1958; Matsuda 1960; Klots 1956). Studies of comparative morphology help detect the homologies and are, therefore, an essential tool for taxonomic and phylogenetic studies.

Although recent studies have been exploring the phylogenetic relationships of the Hesperiidae (Warren et al. 2008, 2009), still much incongruence can be found after the addition of new characters. This study recognizes that the large systematic and phylogenetic confusion in Hesperiidae is due primarily to the lack of basic studies, especially studies of comparative morphology. For this reason, the thorax and abdomen of four Hesperiidae species representing different tribes of the family are illustrated, described and compared, which should complement existing fundamental information for understanding the morphological differentiation of the family, the main objective of this study.

Material and Methods

Individuals of four species of Hesperiidae, representing three subfamilies, were selected: *Pyrrhopyge charybdis charybdis* Westwood, 1852 (Pyrrhopyginae, Pyrrhopygini), *Urbanus teleus* (Hübner, 1821) (Pyrginae, Eudamini), *Pyrgus orcus* (Stoll, 1780) (Pyrginae, Pyrgini) and *Synapte silius* (Latreille, [1824]) (Hesperiinae), as they represent divergent taxa in the family. Thorax body, legs, abdomen and genitalia were boiled in potassium hydroxide (10%), and carefully prepared for illustrations after proper dissection and scales removal. The wings however, were first removed from the dried specimen and then cleared with a fast immersion in 90% alcohol before submersion in a 2.5% sodium hypochlorite solution, until discolored. All illustrations were performed with the aid of a camera lucida, auto-montage pro applications and scanning electronic microscopy. Because phylogenetic relationships regarding to monophyly and status of tribes and subfamilies of Hesperiidae still request further evidences, the classification used in this study follows the taxonomical arrangement (Mielke 2004). As in Carneiro et al. (2012), the morphological terminology used was based on several authors, as discussed below.

Terminology review

Different terms have been used to designate the lines dividing exoskeleton structures in Lepidoptera (Carneiro et al. 2012). Especially in the thorax, the term cleft can be found to designate special delimitations between thoracic sclerites (Matsuda, 1960). Due to its great variability as a character, its use is ignored in the present study, and the term suture being used instead.

Conflicting opinions regarding the location of thoracic spiracles led Madden (1944) to attest their presence in segments II and III, while Ehrlich (1958a), Casagrande (1979a), Bilotta (1994a), and Bizarro et al. (2003a) consider them to be in segments I and II. Based on Hinton (1946) and Stehr (1987), C. Mielke et al. (2004) proposed that their occurrence in segments I and II in the thoraxes of immature individuals might suggest the same origin for adults. Until further clarifications, the first and second spiracles will be used because of their presence in anterior-posterior order, regardless of their origins or location. Following the terminology adopted by C. Mielke et al. (2004), thoracic segments are treated with prefixes pro-, meso-, and meta-, while their sclerites and sutures, repeated in each segments, are indicated with Roman numbers I, II, and III, respectively.

Cervix and Prothorax. The origin of the cervical sclerite is still widely discussed and, to date, there is no consensus whether it would be a modification of sclerites from the head, from the thorax, or from both (Snodgrass, 1935; Matsuda, 1970; Kristensen, 2003). In the present study, these structures are here mentioned for merely practical reasons, regardless of their evolutionary origin.

Seeking to establish homologies between the thoracic sclerites from the different segments, Niculescu (1978) suggested, based on Hesperiidae specimens, that the pronotum was divided into scutum I and scutellum I, among which the patagia and parapatagia would be part of the scutum I and the dorsal bar a part of the scutellum I, which is connected to the pre-scutum II. Sorensen (1980), based on Snodgrass (1935), states that such terminology is applied only to the pterothorax, since the development of these structures are not homologous in the other tagma.

The most prominent lateral sclerite is mentioned in the literature as the episternum (Madden 1944; Freeman 1947; Matsuda 1970; Camargo 1980), the pro-pleura (Niculescu 1978) or the pleura (Casagrande 1979a; Bilotta 1994a; Bizarro et al. 2003a; Kristensen 2003). Its origin is still uncertain, though Michener (1952) and Matsuda (1970) consider it of pronotal origin based on primitive Lepidoptera species, such as

Micropterix Hübner 1825 (Micropterigidae)*, Hepialus* Fabricius 1775, and *Phassus* Walker 1856 (Hepialidae). Freeman (1947) mistakenly used pleuron to designate sternum. The terminology used by Michener (1952) is the one followed in the present study.

In Lepidoptera, the epimeron I is considered absent even though the pleural suture I is present (Snodgrass 1935; Madden 1944). The sclerite was described by Sorensen (1980) as mostly membranous, with a small sclerotized crease that might vary individually in development. Matsuda (1970) considers it as a slim vertical bar that may sometimes be visualized in the Lepidoptera.

As a distinct part of the episternum I (Matsuda 1960), the trochantin I is considered absent in most Lepidoptera, like any other articulation structure located between the coxa and the epimeron (Matsuda 1970). However, Crampton (1920) and Madden (1944) illustrate the presence of the trochantin, Sorensen (1980) and Bilotta (1994a) identify a small coxal pleural articulation in the species observed, and Camargo (1980) illustrates the trochantin and another coxal pleural articulation. Even though Kristensen (2003) doubts the homology of the term as employed by Snodgrass (1935), he refers to the trochantin as present in a great part of the Lepidoptera, although he indicates a great loss of its sclerotization in *Agatiphaga* (Agatiphagidae). Because the visualization of this structure by other authors corroborates the observations in the present study, we use the term trochantin I to designate the articulation sclerite located between the coxa I and the episternum I. In the other segments, no sclerite of this nature was found.

Mesothorax. Three wing processes are found along the ventral margin of the scutum and receive several names in the literature. In this study, the terms anterior notal wing process, median notal wing process, and posterior notal wing process (Sorensen 1980) are used, related to the function of the structure.

Laterally, the episternum II may be subdivided in several topologies, according to the group studied, which generates a number of names, including terms such as: anepisternum, katepisternum, paraepisternum, preepisternum, prepectus, and basisternum. The first two are the most commonly found in the literature, divided longitudinally by the anepisternal suture (Shepard 1930).

Crampton (1914) described the preepisternal suture as located transversally in relation to episternum II, dividing a region anterior to the katepisternum, denominated preepisternum II. Based on Snodgrass (1935), who defines the use of prepectus for the anterior region contiguous to the episternum, Matsuda (1970) drew attention to the erroneous usage of the term preepisternum where secondary sclerotization of the anterior portion of the episternum occurs, along with the complete absence of the preepisternal suture. Brock (1971) reaffirms that this structure, which he denominates paraepisternum, originated secondarily in Lepidoptera through an anterior membranous invagination forming a distinct area between the membrane and the basisternum. Later, Kristensen (2003) confirmed the statements proposed by Brock (1971) and uses the same terminology accompanied by the paraepisternal suture, which is also used in this study.

The presence of the pre-coxal suture (previously denominated by Matsuda (1960) as the para-coxal suture) can be found to be highly correlated with the secondary formation of the para-episternum, and its large variability of forms creates several obstacles to attempts of structure homologation (Brock 1971). Ehrlich (1958a) describes it as the delimitation between the basisternum and the katepisternum, parallel to the paraepisternal (preepisternal) suture, while Matsuda (1960) and Kristensen (2003) use it as the separation itself, between the preepisternum and the katepisternum. Due to the disparity of these structures presented in the species studied herein, such a suture will be denominated as proposed by Ehrlich (1958a). Michener (1952), based on Shepard (1930), adds one more division to the katepisternum, indicated by the presence of the marginopleural suture, which forms a small slender sclerite between the coxa and the katepisternum, indicating that there is no connection between the suture and the trochantin.

The epimeron II, which possesses a large membranous portion, presents an anterior-lateral crease contiguous to the episternum that, though not taken into consideration by Matsuda (1960) as a division, was defined by Shepard (1930) as the preepimeron and its suture was named as the preepimeral suture (described by Shepard 1930) in Madden (1944), Michener (1952), Ehrlich (1958a), Casagrande (1979a), Bilotta (1994a), Bizarro et al. (2003a), and C. Mielke et al. (2004).

Primitively, above the episternum II and the epimeron II, there are two sclerites: subalare and basalare, respectively. The latter having a tendency to migrate to the dorsal area of the anepisternum in some insect groups (Matsuda 1960). The subalare is developed and composed of two plates in Lepidoptera (Matsuda 1960).

Among the articulation mechanisms of the coxa, there is the subcoxal sclerite which, divided into two portions, originates an anterior articulation and a lateral or posterior one, which correspond to the trochantin and to the ventral pleuron or ventropleuron, respectively (Matsuda 1960). The tendency of sclerotization in this area might have favored the disappearance of the trochantin as a structure isolated by membranes, becoming blended to the katepisternum, as it is clearly seen in Dermaptera (Matsuda 1960). The same author describes it as present and contiguous to the pleural suture, like the ventropleuron in Lepidoptera, which should not be confused with the area formed below the marginopleural suture, nor with the basicoxite, which is also mentioned by Michener (1952).

Snodgrass (1935) defines the basicoxite as the coxa basal ring, dorsally detached by the basicostal suture. Some authors (Freeman 1947; Michener 1952; Ehrlich 1958a, 1960; C. Mielke 2004) illustrate the presence of a small triangular sclerite located on the dorsal apex of the coxa, between the epimeron and the episternum, and name it as the basicoxite. According to observations performed with the specimens analyzed herein, the presence of the basicoxite was not observed in any of the coxae, as defined by Snodgrass (1935). The small triangular sclerite, also seen on the species analyzed in this study is, in fact, a superposition and invagination effect of the adjacent sclerites. The insertion point of the external margin of the individual's coxa generates a small pit between the eucoxa, the meron, the katepisternum, and the epimeron, resulting in a surface that could be confused as a differentiated sclerite in some studies. Using scanning electron microscopy (Fig. 54 to 57), the absence of this type of structure is noted, at least in the species observed.

In the ventral region, the median line visualized between the two basisternal structures is denominated discrimen (Michener 1952). Even though, in itself, it is not a suture or any other structure, the line is thus denominated to describe the contact area that originates from the invagination of the entire sternal area of the holometabola, first described by Weber (1928), *apud* Matsuda (1960).

Metathorax. Similar to the mesothorax. The terminology applied corroborates all the information supplied for the previous segment, with the exception of the following: the pleural region of this segment presents a narrower paraepisternum which is not apically differentiated from the basisternum by a suture (Matsuda 1960); and, according to Matsuda (1970), Shepard (1930) denominates the structure located anterior-dorsally to the episternum as the "basalar pad," which would be homologous to the first basalar sclerite as defined by Sharplin (1963a, b). However, Ehrlich (1958a) and Sorensen (1980) call attention to the distinction and presence of this structure anterior to the anepisternum, emphasized by a thin ventral suture. Even though Shepard (1930) had visualized and illustrated both structures, he erroneously named the first and omitted the presence of the second one. Sorensen (1980) also mentions the division of the basalare into three differentiated parts, using the following terms: first basalare, basalare process, and "basalar pad". The terms basalare, due to the absence of the structures designated by Sorensen (1980), and anepisternum are preferred.

Legs. Though Crampton (1920) had mentioned the absence of the basicoxite in all the Lepidoptera observed by him, Michener (1952) describes such structure as evidently separated by a thin suture, internally indicated by a reduced crest. However, the use of this term by the author disagrees with the definition proposed by Snodgrass (1935) who describes it as a round piece on the base of the coxa that interconnects it with the pleural sclerites. Because of the clear difference of the term used by Michener (1952) with the structures observed herein, and following the indications by Crampton (1920), the term basicoxite is replaced by coxal pleural articulation, proposed by Sorensen (1980), who better defines its function in the appendix.

Wings. The analysis is based on the Comstock-Needham system, widely used in the most recent morphological studies. The costal vein, observed and illustrated in many Lepidoptera lineages (Comstock, 1918), and considered to be absent, at least in butterflies (L. Miller, 1970), was clearly seen in the four species as a tubular vein which provides structure to the forewing. On the hind wing, similarly to that described for the *Danaus plexippus* pupa (Comstock 1918), there is the same structure along the humeral angle of the wing. Recently, Kristensen (2003) indicated the presence of 1A on the forewing of several derived Lepidoptera, including Hesperiidae and Papilionidae specimens. However, Comstock (1918) suggested that the loss of this structure is evident by the visible atrophy of the vein in some species studied by him. Due to the absence of justifications for the changes in terminology, the terms suggested by Comstock (1918) are used herein.

Abdomen. All the segments corresponding to this tagma are attributed to this section, except those distinctly modified for the formation of the genitalia. Snodgrass (1935) and Kristensen (2003) disagree with respect to the location of the abdominal spiracles, the former mentioning its occurrence in the tergum and the latter in the pleural membrane. According to Snodgrass (1935), its identification should be based on the visualization of the dorsal-pleural line instead of using the sclerotization patterns of the sternal, tergal, and/or lateral-tergal sclerites, which, according to the author, significantly vary amongst several insect orders. Because of the complete fading of this line, and the impossibility of visualizing it in all the specimens studied herein, only the presence of such a structure in the pleural membrane is indicated, ignoring the origin and modification of the structures.

Male Genitalia. The term vinculum is omitted here due to the indication by Pierce (1916), who suggests that this term (established by him in 1909) is synonymous of saccus, which had previously been used by Bethune-Baker (1891). The area could be clearly identified as the fusion of two projections of the sclerites corresponding to the ninth abdominal segment. In the present study, the favored terms are: saccus, lateral-dorsal projections of the saccus, and lateral-ventral projections of the tegument.

Due to the same arguments defended by Niculescu (1973), priority is given to the term futura inferior instead of juxta. According to the author, the denomination proposed by Peterson (1904) is anterior and homologous to the one usually found in the literature (Klots 1956), the reason for its use in this study.

Different reviews of the male genitalia terminology have been proposed in Lepidoptera, given its importance to species identification (e.g. Petersen 1904; Eyer 1924; Sibatani et al. 1954; Ogata 1957). However, they disagree specially regarding the subdivisions of the valva. Nowadays, the valva terminology usually applied are those reviewed in Sibatani et al. (1954) and Klots (1956), which were also applied in this study, such as: costa (dorsal-basal portion of the valva), sacculus (ventral portion of the valva) and harpe (posterior projection of the sacculus, observed on the internal face of the valva).

The ampulla, first described in Noctuidae as a dorsal-posterior projection of the internal face of the valvae (Pierce, 1909), can actually assume different positions and development within different groups of Lepidoptera (Sibatani et al. 1954). Therefore, determining its homology among various groups can be seriously challenging. Specifically within the Hesperiidae, this structure has been indicated to represent "complicated secondary structures" (Sibatani et al. 1954), which is hardly comparable with the original description of Pierce (1909), given the great modification of genitalia structure between both these families. Since no similar structure was found in this study, we preferred to omit the term ampulla in our descriptions, even though it is regularly used in skipper genitalia.

Oiticica (1946) observed a great number of penises of Lepidoptera from a broad sampling of lepidopteran groups, and presented a special terminology. His prerogatives for the use of the term penis in its broad meaning (including bulbus, ejaculatory duct, aedoeagus, and vesica) are accepted and used in this study. The other terms used here are applied following proposals by Klots (1956).

Female Genitalia. Despite being followed in morphological sutdies (e.g. Klots 1956), the term genital plate used by Pierce (1909) is here replaced by sterigma. This choice was made as the term sterigma implies the fusion of the ante- and post-vaginal lamellae. Moreover, it is more commonly found mentioned in the literature and widely used by specialists. For the other characters of the female genitalia, all the terms adopted by Klots (1956) are used.

Results

Pyrrhopyge charybdis charybdis Westwood, 1852

Cervix and Prothorax. The cervical sclerite is composed by a pair of T-shaped slim sclerites whose bases are inserted into the episternum. It possesses two pairs of ventral-anterior arms, the dorsal pair is long and connected to the concavity of the tentorial bridge, while the ventral pair is about half the size of the dorsal and does not blend ventrally (Fig. 1). In the second basal quarter of the dorsal arm, there is a well developed sensitive cervical organ (Ehrlich 1958a), containing relatively long bristles, and denominated cervical organ.

The first thoracic segment is reduced to small sclerotized areas within the pleural membrane, anteriorly delimited by the cervical sclerite and posteriorly, near the spiracle, by the scutum II and the epister-

num II. The notum has two lateral plates and a dorsal plate (Fig. 1 and 5), the latter being lobular, posteriorly elongated and dilated on the posterior margin, presenting a distinctly sclerotized central line, bifurcated on the middle, forming a distinctly melanized triangular posterior area. The lateral plates are anterior-posteriorly flattened, reaching the apical portion of the episternum.

Posteriorly, the patagia form slightly bulging sclerotized lobes between the head and the thorax, articulated on two points with the dorsal prothoracic membrane, and carry scales that cover all the cervical-prothoracic area. Likewise, the parapatagia, which are also sclerotized, are located over the membrane and extend lateral-ventrally towards up to near the first thoracic spiracle, which is elongated and located on the pleural membrane. The surface of the parapatagia presents two bands with distinct sclerotization and texture, the anterior is rugged and slightly translucent, and the posterior is more melanized, hard and smooth, without insertion of scales. Additionally, a pair thin bars, parallel to the parapatagia, is found on the posterior limit of the dorsal membrane of the prothorax, anteriorly to the prescutum II and the scutum II (Fig. 5). Most likely, due to its frailty and difficulty in visualization, no mention of this structure by other authors was found.

The episternum I is oval, ventrally delimited by the articulation with the trochantin, and dorsally by a slightly more melanized region that is also distinct, which is connected to the lateral bar of the pronotum. Its lateral-posterior portion presents an internal crease, which might be a manifestation of the pleural suture of the epimeron I or can be characterized as a simple crease of the episternum (also visualized in the mesothorax). The trochantin I (Fig. 1, 9 and 62), a small elongated structure which is also near the preepisternum, is located between the coxa and the episternum.

Anteriorly, the preepisternum I forms a convex shield anterior-ventrally to the episternum I, and is ventrally projected as a slim extension which is posteriorly connected to the furca I. Ventrally (Fig. 9), this structure forms a triangular plate, where there is a unique concavity, which forms two internal apophyses for the adhesion of thoracic muscles responsible for part of the leg movement. It is posteriorly connected to the spina I, which connects the prothoracic segment to the metathoracic one via two long structures, forming an articulation similar to a spring. This mechanism allows all of the tagma to be adhered to the mesothorax, offering more support to a segment that is formed, to a great extent, by membranes. Posteriorly, it is articulated to the paraepisternum II through small slim articulations.

Mesothorax. The notum II is divided into four sclerites: prescutum II, scutum II, scutellum II and postnotum II. The first forms a triangular structure (in dorsal view) blended to the scutum by the prescutoscutal suture (Fig. 13). Laterally, its view is blocked by the anterior-lateral development of the scutum II and by the concavity of its anterior-ventral margin (Fig. 17). The scutum II covers great part of the thorax, and forms an elongated dorsal hemispheric capsule that laterally presents three apodemes and a sulcus along each side of the weak mesoscutal suture. A pair of oblique sulci occurs median-laterally, which might be related to movement and/or support of the tegulae. Posteriorly, the W-shaped scutoscutellar suture II separates the scutum II from the scutellum II, posteriorly giving a bilobed appearance to the former.

Laterally-ventrally, three processes surge for the articulation with the axillary sclerites, two from the scutum II (anterior and median) and the other from the scutellum II (posterior). The anterior one, the anterior notal process II is wide, strongly developed towards the subalare and separated from the scutum by an evident suture. The smaller median notal process II, composed of a bidentate projection, with the posterior apophysis which is more developed and anteriorly projected, under the small anterior dentation. The posterior notal process II, originating from the anterior arm of scutellum II, forms a simple and small expansion and its internal portion connects to the median process via a suture that is not visualized laterally, nor is it mentioned in any morphological descriptions from the literature. The median notal process II, which is difficult to visualize, is sometimes omitted in a few illustrations found in the literature.

The scutellum II, which is imbedded between the scutum II and the postnotum II, reaches the posterior portion of the thorax, dorsally covering the scutum III and the postnotum II itself, which is ventrally hidden (Fig. 17). Lateral-anteriorly, two parallel arms meet the post-wing portion of the epimeron II and the anterior arms of the postnotum II. The axillary cord II rests along this arm. The phragma II, which is blended to the postnotum II, extends ventrally-posteriorly (entering part of the first abdominal segment) as a convex shield where muscles responsible for moving the wings are inserted. Its surface contains tegumental creases which dorsally blend to the internal creases of the scutum III.

The subtegula is elongated, dorsally circling the basalare II, located on the pleural membrane, between the anepisternum II and the anterior notal process of the wing. Posteriorly, the subalare II plate is well developed and completely surrounded by the pleural membrane. Its anterior-posterior ends are sharpened and separated, in the median area, by a transversal suture. The tegulae, located dorsal-laterally to the mesothorax, form mobile lobed structures, articulated to the subtegula by a circular orifice located on its inferior face (Fig. 21), where a short median suture is originated, although not observed in the other species.

The anepisternum II is approximately square-shaped (Fig. 54), and partially blended to the katepisternum II through the anepisternal suture II, which has approximately 3/4 of the width of the katepisternum II. Dorsally, it presents a tegumental crease that is directed towards the interior of the body. The longer katepisternum II is ventrally extended, and is partially blended to the basisternum II due to the presence of an incomplete and apically curved paraepisternal suture II (Fig. 9). The anterior portion of the katepisternum II is arched towards the internal part of the body and it is weakly delimited by a suture, especially on the dorsal-anterior portion. The paraepisternum II is triangular, presenting a small invagination on the median-posterior region so that it can articulate with the spina I.

The marginopleural suture II is short, originating on the coxal suture and directed towards the basisternum II, ending at the discrimen II. The basisternum II is triangular, dorsal-ventrally flat, longitudinally sectioned by the discrimen II. It tapers off posteriorly into a median crest, which connects itself internally with the furca II projections (both diagonally project themselves inside the body and blend with the postalare region of the epimeron II). In the ventral portion of the furca II, there are a pair of small projections, the coxal ventral articulations II, which are responsible for the connection of the internal margin of the coxae II to the pleural sclerites. Coxopleural articulations II are visualized through a depression on the dorsal portion of the eucoxa II and the meron II, connected to the basicostal suture.

The epimeron II is irregular, possessing a membranous dorsal portion and an anterior membranous transversal lobe projected on the epimeron II, which, in lateral view, covers a narrow extension parallel to the pleural suture II of the epimeron II, itself (Fig. 17). Posteriorly, its dorsal margin is undulated. There is an additional tegumental crease, directed towards the inside of the body (which connects ventrally to the furca II projection), and there is yet another small triangular membranous portion ventrally, next to the meron II.

Metathorax. It is similar to the mesothorax, basically being made up of the same structures, though different in shape and size. Two concave triangular plates, median-posteriorly connected by a thin extension, form the scutum III, located lateral-ventrally to scutellum II. It presents two ventral projections directed towards the pleural membrane: anterior notal process III and posterior notal process III (Fig. 25).

The scutellum III and the postnotum III are anterior-posteriorly flat, and precede the first abdominal tergum. Lateral extensions of the scutellum III, which support the axillary cord III, stretch out parallel to scutum III, while the postnotum III extends laterally along the epimeron III. The basalare III is small and thin, and offers support to the hind wing.

The anepisternum III, which is separated from the katepisternum III, is oval and hides the spiracle II. The katepisternum III is semi-trapezoidal and ventrally-anteriorly separated from the paraepisternum III by the paraepisternal suture, as well as by a tegumental crease that fixes this structure to the other anterior sclerites of the mesothorax. A crest on the internal side of the katepisternum can be seen by transparency, dorsally-ventrally crossing the katepisternum III, where a bundle of muscles directed towards the hind wing is attached to it. Perpendicular to the pleural suture III, there is the complete marginopleural suture, forming a triangular sclerite right above the eucoxa III (Fig. 25). Ventrally, there is no suture that separates the katepisternum III from the basisternum III (Fig. 9).

The epimeron III is geometrically similar to the epimeron II and ventrally presents a longitudinal suture that separates it from a narrow triangular sclerite, which contains a non-sclerotized ventral portion. Such a division of the epimeron III was not found in any other species (Fig. 25).

Legs. The anterior pair is smaller, without any modifications or reduction of sclerites in any of the five articles. They do not present a basicostal suture. The coxa I is long and tubular, with a slightly wider base, without any evident articulation points on its internal dorsal margin (Fig. 29). The articulation zone with the trochantin I does not present any evident differentiation. The trochanter I is triangular, small, and presents a dorsal concavity. The femur I is tubular and a little longer than the coxa. The tibia

I is less than half the length of the femur I, and is provided with a baton-shaped, internally curved, median epiphysis, which is probably related to the antenna cleaning behavior (Fox, 1967). The tarsus I is composed of five tarsomeres, the proximal one being larger than the others (by around six times). The fourth tarsomere is smaller in males and even smaller in females. Along the entire tarsus, three series of ventral thorns of different sizes are present. The last tarsomere presents few and small lateral-ventral spines, has almost no scales and is provided with a pair of sensitive bristles at its apex area.

The other pairs of legs maintain basically the same aspect, though the coxae II and III are subdivided into eucoxa II and III (anterior ones) and meron II and III (posterior ones) by the basicostal suture II and III, respectively. They are slightly curved and dorsally contiguous to the pleural sutures II and III (Fig. 17, 25 respectively). These coxae are conical, a little shorter than the anterior coxae, unlike tibias II and III, which are longer on the mesothoracic and metathoracic legs (comparatively to the femurs) and possess spurs at the same position as the epiphysis on tibia I, a pair of mesothoracic apical spurs on tibia II and a pair of apical spurs plus a pair of mesothoracic subapical spurs on tibia III, all of which are asymmetrical (Fig. 29).

The distitarsus is similar in all legs, presenting arolium, pulvilli, and tarsal claws intermingled with the unguitractor plate, which is cylindrical and short. The arolium is connected to unguitractor plate by a fan shaped and vertical stretched peduncle, which is apically dilated. The tarsal claws are bifid, presenting a curved and needle-like apical projection, while the base is truncated next to the pulvillus, which is also bifid and presents small bristles (Fig. 58).

Wings. Triangular mesothoracic wings presenting fourteen longitudinal veins, of which only the 3A vein does not extend up to the margin (Fig. 33). The costal vein (C) extends from its insertion at the base until it anastomoses with Sc (Fig. 39). In the remaining costal portion of the wing, its presence is dubious and deserves detailed histological studies. The Sc vein freely originates on the base of the wing without branching, ending a little over half the length along the costal margin. The radial vein also parallel to coastal margin and super-exposed at its base, has all its branches differentiated starting from the main branch, except for M1, which, in males, is originated next to the bifurcation of R4 and R5, while in females its origin lays anteriorly.

The discal cell is elongated (Mielke, 2001), longer than the anal margin or more than 2/3 of the size of the costal margin. At its apex there is a thin and small prominent vein (dcs) which is joined to the base of the M1 and then branches in the medial portion of the M2 vein. The dcm vein is slightly longer than the dci, making the origin of M2 closer to M3 than to M1. The dcm and dci veins are barely visible and completely close the discal cell on its distal margin. In the posterior area, the 2A and 3A veins originates independently at the base of the wing, the latter blending with 2A near the first ramification of the cubital vein.

The metathoracic wings present softer angles and only eight longitudinal veins. The costal vein provides structure to the humeral angle, continuing towards the bifurcation of Sc and R. It is dorsally adorned of differentiated scales that are similar to those on the ventral anal area of the mesothoracic wing (Fig. 42 and 43). Sc, R, and CuA originate from a single branch, after which the first vein to diverge is the Sc+R1 which extends to the apical angle of the wing. Rs is also parallel to the costal margin and originates from the base and from the Sc+R1, bifurcating from M1 before the apex of the discal cell. The CuA vein is similar to the forewing. However, the dcm vein does not originate from M2, which is absent. The 2A and 3A veins are again separated at the base and end at the anal angle of the hind wing. There is no evident humeral vein, though there is a small projection directed towards the base.

Abdomen. It is thick and fusiform, and is represented by ten segments. Due to the reduction of the last two or three segments to form the genitalia, only eight segments in males and seven in females are visible (Fig. 66 and 67). The number of segments follows the number of spiracular orifices in the pleural region, the first pair being relatively more developed than the others, and partially covered by the tergal lobe. There is no spiracular orifice in the eighth abdominal segment of males.

Anteriorly, the tergal lobe is characterized as a circular evagination of the membrane, which is slightly sclerotized and projected over the first spiracle (its location may be influenced and effected by the specimen preparation). The prespiracular bar is thin and articulated to the sternum by a small ventral concavity that separates it from the anterior-lateral apodeme of the first sternite. Dorsally, the prespiracular bar does not reach the tergopleural bar. Likewise, the postspiracular bar, which is reduced to a lateral-ventral extension of the second tergum, does not reach the dorsal margin of the sternum. Over the first

tergum there is also a bar (tergopleural bar), which is blended to the anterior-lateral margin of the second tergum and responsible for the sclerotized integumental connection between the abdomen and the thorax. Longitudinally, the tergopleural sulcus traverses the tergopleural bar, which is positioned ventrally to the first tergum.

The first tergum is anterior-posteriorly compressed between the thorax and the second tergum, which gives it a scale-like shape (De Jong et al. 1996; Ackery et al. 1999; Mielke 2001). In the first and second sterna (topographically blended sclerites) it is possible to see a small median ventral prominence similar to a keel, which gradually disappears posteriorly on the other abdominal sterna.

The subsequent terga are partially juxtaposed to the posterior ones, following the schematic aspect of secondary sclerotization proposed by Snodgrass (1935). The entire dorsal-distal tergal portion located on the posterior tergum is membranous. The sterna do not present such a conformation.

The other pregenital segments, although basically similar, do not present specializations or substantial changes in their external morphology, except for the last one (eighth in males and seventh in females), which presents significant differences, including sexual dimorphism. The pregenital segment presents a tergum provided with a membranous posterior invagination, which is semicircular in males and C-shaped in females (Fig. 74 to 77). The sternum is distinctly reduced in males to a small sclerotized thin bar, while in females it is rectangular and has round edges. There is a thick spot on the posterior margin of the terga where long bristles, which reach the base of the genitalia, are inserted.

Male Genitalia. The two terminal segments of the male are modified for the formation of the genitalia, the ninth tergum corresponding to the tegument, the sternum to the saccus, and the tenth to the uncus and the gnathos. Dorsally, the tegument forms a bulging structure on the dorsum, provided with posterior-lateral bifid apophyses, which are developed, strongly sclerotized and projected in parallel towards the uncus, which is also bifid (Fig. 98). Ventrally, a M shape membranous orifice can be seen on the uncus. The gnathos can be observed as being composed of a pair of triangular parts glued to the membrane and presenting a thin longitudinal expansion that gives ventral support to the anal orifice. The fultura inferior is distinctly developed on a lobular plate, flattened on the median-frontal area and present a strong dorsal depression, which is responsible for supporting the aedoeagus (Fig. 102).

The saccus is anterior-dorsally projected as a lobe, reaching about half way up the ninth segment. It is curved parallel to the basal portion of the valva, containing a small lobe over it (Fig. 90). The lateral-dorsal projections of the saccus continue until they blend with the tegument, on its lateral-ventral projections.

The valva is well developed, somewhat bulging, anteriorly narrow, dilating posteriorly to the insertion point of the tegumen. The harpe covers all the internal apical face of the valva, slightly pointed posteriorly until it reaches a round apex which is provided with a cluster of relatively long bristles; its dorsal margin is full of small spines, as well as an evaginated arm sheltered between it and the large basal portion of the valva, forming a crease in the median portion of the valva. The homology of this crease with the ampulla described by Sibatani et al. (1954) is discredited, once this crease originates directly from harpe. In the median area of the valva there is also an almost oval-shaped internal orifice, from where the membranous creases inside the valva are viewed. The costa is represented by a posterior crease of the valva, next to the harpe, which is absent on the dorsal margin of the valva. The sacculus is well developed and surpasses more than half the height of the entire valva (Fig. 91).

The aedoeagus is relatively small and thin (Fig. 106). Anteriorly to the opening of the ejaculatory duct there is the *coecum penis*, which is developed, semi-oval, and slightly curved dorsally to the right. The ejaculatory bulb is globular and membranous. On the opposite end, there is a small triangular crease turned to the right (Evans, 1951), which presents small apical spines and covers the base of the vesica, which is oval, long and does not present cornuti.

Female Genitalia. Composed by the eighth, the ninth, and the tenth abdominal segments, the whole female genitalia forms two main structures: the isolated eighth sternum and the anal papilla (represented by the ninth and tenth segments). The former is surrounded and sustained by the strong sclerotization of the vaginal lamellae, which, in this case, form a tubular sterigma, where three extensions are present in its opening, two aculeate dorsal ones, and a truncated ventral one (Fig. 110 and 114). It is possible to observe a great variation in these extensions of the sterigma, which need further studies in order to infer about its importance in the differentiation of species or populations.

Laterally to the sterigma duct there is another pair of strongly sclerotized and pointed spines that reach about half the length of the duct, and are fixed to an also sclerotized lobe which is laterally articulated to the duct. Dorsally, the arched projection of the sterigma reaches the ventral portion of the anal papilla and possesses an apically circular orifice whose function is yet unknown. The eighth tergum occurs anterior-dorsally, and is distinctly reduced and almost completely blended to the dorsal portion of the sterigma.

From the duct of the bursa, a dilatation is developed anteriorly to the body that is denominated cervix of the bursa, which precedes the bigger, oval, completely membranous and without signa dilatation, which is the denominated corpus of the bursa. It was not possible to observe the presence of spermatophores among all the specimens observed. The anal papilla corresponds to two lateral plates which together form a cylinder external to the anal (dorsal) and vaginal (ventral) orifices and are apically covered by several bristles.

Urbanus teleus (Hübner, 1821)

Cervix and Prothorax. Similar to those observed in *Pyrrhopyge charybdis charybdis*. The anterior-dorsal projection is slightly longer and the cervical organ is slightly smaller (Fig. 2), bearing small bristles as in *Epargyreus clarus* (Pyrginae, Eudamini) (Cramer, 1775) (Ehrlich 1960).

The anterior lobe of the dorsal plate is cordiform, with a more sclerotized spot on the anterior margin, and a crease with darkened cuticle on the anterior-lateral third of the projection directed towards the prescutum II (Fig. 6). There is a terminal dilatation with the convex margin.

The parapatagia present a slightly sclerotized anterior band, being confused in some areas with the membrane itself. The dorsal apex fits into the crease of the notal extension (Fig. 2). The trochantin I is rectangular, posteriorly directed, located between the preepisternum I and the episternum I (Fig. 63). Other prothoracic structures are similar to those in *Pyrrhopyge charybdis charybdis,* varying in shape and size to a small degree.

Mesothorax. Despite its length being close to that of *Pyrrhopyge charybdis charybdis*, it is distinctly smaller in width, which permits the ventral and dorsal identification of pleural sclerites which were not visualized in the previous species (Fig. 10 and 14). Consequently, the scutum II is slightly longer, presenting less conspicuous oblique sulci and a smoother scutoscutellar suture II.

The anterior notal process II is less developed, in comparison to the previous species, and ventrally directed, without curvature at the apex. The median notal process II is almost entirely hidden under the pleural membrane and is joined to the posterior notal process II (Fig. 18).

The postnotum II with a larger dorsal portion hidden under the scutellum II, and differs little from the previous species. The arms of the scutellum II are also very similar in structure, as well as in the fitting mechanism between the postnotum II and the epimeron II.

The subtegula II is long, though it does not dorsally circle the basalare II, being located anterior to it. The subalare II, presents a shortened posterior thinning, with the suture being posteriorly dislocated.

The tegulae are similar to the previous species and receive on their inferior face a developed membranous area which covers a large part of the subtegular sclerite (Fig. 22). The anepisternum II is a little longer (Fig. 18), separated from the katepisternum II by the anepisternal suture II, which is shorter (around half the width of the episternum II). The katepisternum II, the basisternum II, and the prepectus II present a strong similarity in their structure to those of the *Pyrrhopyge charybdis charybdis*, with the exception of the sternopleural suture, which is incomplete and straight, without curvature at the apex. Likewise, the coxal suture II is incomplete and forms a blended area near the basisternum II (Fig. 10). The coxal ventral articulations II are on the median crest, located ventrally-laterally to the discrimen II. The epimeron II is similar to that in the previous species, except for the presence of a pair of parallel transversal sutures found on a small membranous area between it and the meron II (Fig. 18).

Metathorax. Little structural differences can be found in this tagma in comparison to the previous species, all of them being reduced to the pleural-sternal region. In the katepisternum II, the internal crest is located more ventrally, forming a dorsal triangle relatively larger than that of *Pyrrhopyge charybdis charybdis*. The marginopleural suture III is incomplete and does not reach its ventral portion in its margin with the eucoxa III. Anteriorly, the paraepisternum III is prominent and clearly visible in lateral view (Fig. 26).

The epimeron III presents a membranous spot, in the shape of a hook, which is invaginated in the dorsal margin of the sclerite. Inconspicuous in some of the specimens observed, its presence might be related to individual variations or even to the boiling time of the specimen in KOH, which might modify coloration and consequently its distinction.

Legs. The legs are slightly longer and thinner than *Pyrrhopyge charybdis* (Fig. 30). The fifth tarsomere has no ventral thorns and scales on the anterior pair, presenting five long bristles on all of the articles, inserted on the dorsal face.

The segments are basically similar, with small differences in shape and proportion in each of them. The basicostal suture II is not contiguous to the pleural suture, even though they are interconnected by a small extension of the precoxal suture II (Fig. 18). The tibias II present a pair of small thorns on the external face, located between two pairs of spurs (Fig. 30). The meron II is dorsally-ventrally divided by a suture similar to that found on meron III in *Pyrrhopyge charybdis charybdis*, between the epimeron II and the meron II, without a membranous area. In contrast, the meron II does not present this same division (Fig. 26). The distitarsus presents two pairs of ventrally curved apical bristles. The other characters are similar to those in the previous species (Fig. 59).

Wings. The wingspan is approximately 35 mm in males and 39 mm in females. The wing margins are straighter and the angles (apical and posterior) are more acute (Fig. 34). The mesothoracic wings are similar to *Pyrrhopyge charybdis charybdis*, except for vestiges of M_3 (recurring vein) turned towards the inside of the discal cell. The discal cell is approximately the size of the anal margin or equal to 2/3 of the length of the costal margin. The M_3 vein is originated closer to M_2 than CuA_1. The 3A vein is directed and blended to 2A, though anteriorly to the first ramification of the cubital.

The hind wings are relatively larger, presenting anal projections ("tails") with approximately the length of the wing's width, and are supported by the extension of the 2A. The m-cu vein is twice the size in females than in males, looking like a small spine directed towards the base.

Abdomen. The tergal lobe is more sclerotized and also projected over the first spiracle (Fig. 68 and 69). The prespiracular bar can be considered as absent or completely blended to the apodeme of the first sternum. It is slightly arched and does not dorsally reach the tergopleural bar either, the latter being thicker than in the previous species. The postspiracular bar, which is almost inconspicuous, is reduced to a little prominent aculeate projection directed towards the pleural membrane.

The first tergum is distinctly widened, even though it is reduced over the tergopleural bar and between the thorax and the second tergum. The sterna suffer a considerable reduction on their lateral-dorsal extensions, especially in females, where the structure becomes even more reduced. The keel-like appearance is similar to that in *Pyrrhopyge charybdis charybdis*, though it is smoother.

The last pregenital segment in males presents an arched anterior margin of the tergum (Fig. 78 to 81). The corresponding sternum is also anteriorly arched and presents a small median recess on its anterior margin. In females, the sternum is semi-oval, and contains a triangular membranous invagination on the anterior margin.

Male Genitalia. Tegument without posterior apophyses and posterior margin truncated (Fig. 92 and 99). The uncus is bifid with rounded arms. Ventrally, the membranous opening has a semi-oval shape. The gnathos, which is distinct, is represented by a pair of slim tubes, which are slightly arched on the sides. The fultura inferior is V-shaped with dorsal projections slightly dilated apically (Fig. 103).

The saccus has no developed anterior projection, measuring around ¼ of the length of the ninth segment and dorsally blended to the lateral-ventral projections of the tegument. The anterior margin is curved and parallel to the margin of the valva, without superimposing on it.

Also presenting a thin base, the valva has a semicircular anterior portion with long bristles in the middle, which are probably related to pheromones or to mechanical functions during copulation (Fig. 92). The harpe is posteriorly differentiated at the tip of the valva, and possesses, besides several ventral bristles, a group of anterior-dorsal spines, which are posterior to a large and well developed dorsal spines (Fig. 93). Internally, it is possible to visualize the sacculus which is reduced to a third of the height of the valva and provided with thicker bristles on its dorsal-posterior surface. Similar bristles are also visualized on the internal dorsal-posterior margin of the valva, standing apart from the thick bristle coverage on most of the structure's internal surface. The costa is reduced to a triangular crease of the dorsal margin of the valva, which is not prominent.

The aedoeagus is more developed both in length and thickness (Fig. 107). On its anterior end, the aedoeagus' coecum is also developed and arched, though thinner and directed towards the left. The ejaculatory bulb is oval, being separated from the aedoeagus by an ejaculatory duct of similar size. On the posterior end, the vesica distally hosts a spine-shaped cornutus, which is long and sclerotized, besides an aculeate extension of the aedoeagus which is flat and ventrally arched.

Female Genitalia. The sterigma is composed of the coupling of the antevaginal lamella with the postvaginal lamella, which forms a U-shaped arch, forming between them a ventral-posterior cavity which hosts the ostium bursa (Fig. 111 and 115). On the median-anterior region there is a portion with less sclerotization, where the two plates blend. The eighth tergum is narrow and entirely adhered to the terminalia, connecting to the papillae on their lateral-ventral surface.

The body of the bursa is cylindrical and twice as long as the sterigma and connected to the ostium by a short duct that is devoid of any dilatation. The internal spermatophore is strongly sclerotized, equipped with an anterior semicircular pouch and an extension that follows the contours of the bursa, and is recoiled inside it. An opening is found next to a pair of parallel sheaths and is directed towards the duct of the bursa.

The anal papilla is slightly sclerotized anteriorly, forming two differentiated sclerotization patterns. A pair of posterior apophyses connects to its anterior margin and gives support to the movements of the genital apparatus.

Pyrgus orcus (Stoll, 1780)

Cervix and Prothorax. Cervix as in *Urbanus teleus* (Fig. 3). The prothorax similar to that of *Urbanus teleus*, being different only in its smaller size (which is proportional to the entire size of the individual), and by the crease on the first third of the posterior extension of the dorsal plate of the pronotum, which is not as evident and does not present distinct sclerotization (Fig. 7). The anterior portions of the parapatagia are more defined from the adjacent membrane and slightly narrower, proportionally (Fig. 3). The posterior part of the spine I is distinctly wider forming a triangular plate with the anterior apex curved towards the inside of the body, as in the other species.

Mesothorax. Among all the species observed, *Pyrgus orcus* has shown to be the slimmest, presenting a certain lateral flattening in males (Fig. 15). In females, this characteristic is less evident. The prescutum II is reduced in its width. The scutum II and the scutellum II are more melanized, which makes it difficult to visualize some of the structures. The median-lateral sulcus of the scutum II is less prominent, or sometimes inconspicuous.

The notal processes II are similar to those in *Urbanus teleus*, with the exception of the first one, which despite its proportional size and shape, is laterally directed, in contraposition to the body cavity (Fig. 19). The subtegula is relatively smaller in length, and as in *Urbanus teleus*, reaches its posterior margin on the anterior margin of the basalare II. The subalare II does not present a thin posterior projection.

The tegulae, which are relatively larger, present a more prominent dorsal-anterior margin than in the previous species, and are located along the sides of the subtegular sclerites, which are slightly reduced (Fig. 23).

The anepisternum II is delimited by an anepisternal suture II, with the same size, as in *Pyrrhopyge charybdis*(Fig. 52). Ventrally, the katepisternum II is partially blended to the basisternum II, as observed in *Urbanus teleus*, as its coxal suture is similar to it and the marginopleural suture II is equally incomplete. Posteriorly to the basisternum II, there are the ventral articulations of the coxa II, which are also located after the discrimen II (Fig. 11).

The epimeron II is not different in shape from the previously mentioned species. However, present a distinct suture in the anterior portion towards the integumental crease, which could represent a probable differentiation from a preepimeron, thus being denominated preepimeral suture II (Fig. 19).

Metathorax. Similar to *Urbanus teleus*, it possesses the same differences in the internal crest, the marginopleural suture III and the paraepisternum III. The spot on the epimeron III was not visualized in any of the specimens observed (Fig. 27). Males present a pair of cuneiform glandular pouches carved in the internal margin, which originate in a narrow membranous band between the epimeron III and the meron III. They are glandular structures associated to a brush of odoriferous bristles located on the

tibiae (Barth 1960). Laterally, it is possible to observe that the meron III is reduced in width by the development of the eucoxa III. The basicostal suture is equally developed, as in the previous species.

Legs. The legs are smaller, due to the reduced size of the individuals of this species (Fig. 31). The femur I presents a smaller relative length, around 1.5 times the length of the tibia I. The coxa II presents a basicostal suture II not contiguous to the pleural suture II, intermingled with the pre-coxal suture II by a distance twice greater than the one observed in *Urbanus teleus* (Fig. 7). In the posterior pair, the basicostal suture II is reduced, observed only through a slightly curved sulcus, posteriorly dislocated and discontinuous from the pleural suture III. The triangular sclerite is observed, in this case, as it is in *Urbanus teleus*, present in the meron II and absent in the meron III. The arolium is trifurcated, with two sharp dorsal projections and the ventral truncated as those found in the other species (Fig. 60). The tarsal claw presents a ventral projection in the shape of a spine.

Wings. Both males and females present similar variation in wingspan length, with approximately 25 mm. The forewings are widened and triangular, with the discal cell a little longer than half the costal margin (Fig. 35). Between the C and the Sc, there is a group of differentiated bristles, located on a tegumental crease, denominated costal folds (Barth 1960), a secondary sexual character of males in certain Hesperiidae (Pyrginae).

The dcs vein is difficult to visualize because of its transparency, which is similar to dcm and dci, and there is no significant sexual differentiation in the distance of the insertion of M_1 with $R_4 + R_5$. The discal cell is 1/5 smaller in length than the anal margin, or around half the length of the costal margin.

The 3A vein is twice the length in males than in females, and both do not extend past half the length of the CuA until its first bifurcation. In this species, it is possible to observe a small continuous projection of the 3A toward the external margin.

The hind wings present distinctly elongated scales on the costal margin (Fig. 47). The M_2 vein is thin, occurring from the middle of M_1 and M_3, inserted in the junction between dcs and dci. There is sexual dimorphism in the m-cu and in the humeral vein, as in *Urbanus teleus*.

Abdomen. It is fusiform and laterally flattened (females present a smaller degree of flattening) (Fig. 70 and 71). The tergal lobe is weakly sclerotized, similar to a lobe detached from the membrane and located on the first spiracle. All the bars that circle the spiracular opening of the first abdominal segment are similar to those in *Urbanus teleus*. The first tergum is distinctly developed, located above the tergopleural bar. The sterna are strongly reduced to small ventral plates, and devoid of the lateral-dorsal extensions which are well developed in *Pyrrhopyge charybdis charybdis*, or reduced in *Urbanus teleus*. There are no ventral prominences in the sterna in *Pyrgus orcus*.

The last pregenital segments do not present a membranous recess in both sexes (Fig. 82 to 85). The eighth tergum in males is reduced to a triangular plate with bristles concentrating on its small apical angle. The sternum is reduced laterally and anterior-posteriorly, forming a small ventral square plate, with little sclerotization. In females, the tergum has an inverted trapezoidal shape, while the sternum is anterior-posteriorly elongated.

Male Genitalia. The tegument longer, covering over half the extension of the valva, and presenting slightly sclerotized lateral-ventral projections that connect median-ventrally to the gnathos (Fig. 94). The uncus is cordiform, full of dorsal bristles, parted in the middle by a membranous fenestra visible in dorsal view (Fig. 100). Ventrally, there is only one median line separating the two symmetrical structures located posteriorly to the triangular membranous orifice, which is contiguous to the rectangular opening observed between the tegument and the gnathos. The gnathos is spatula-shaped, highly sclerotized, full of setae on its surface, and is inserted on the ventral surface of the anal duct. Under the gnathos rest a triangular structure, also connected to the tergum by two thin dorsal projections which are inserted next to the ventral projections of the tegument. This sclerite is denominated fultura superior and was not found in other species studied. The fultura inferior has the same V-shape format of that in *Urbanus teleus*, although shorter and with an oblique inferior edge (Fig. 104).

The saccus is slim, anteriorly extended, reaching 1/3 of the length of the ninth segment and does not present dorsal-anterior projections. Dorsal projections of the saccus and ventral projections of the tegument are similarly blended, forming a single annular piece. The valva is similarly developed, presenting a strongly sclerotized but reduced harpe, full of bristles on its anterior margin (Fig. 95). The ampulla, as described to Palearctic species of *Pygrus* (De Jong 1972), is not present. The sacculus is less prominent, though it presents long thorns on its posterior end. The costa is manifested as a tegumental crease of the

dorsal margin of the valva, covered by bristles over all its extension, without membranous spots on its surface.

The aedoeagus follows the same shape pattern presented in *Urbanus teleus*, only slightly thicker (Fig. 108). Anteriorly, the aedoeagus' coecum is thin and does not present a considerable arch. The ejaculatory bulb is oval, without tubular shape next to the aedoeagus opening. In the posterior end, a group of small spines is ventrally observed on the right side, next to the orifice of the vesica, opposite to a single well developed and strongly sclerotized spine. Ventrally, there is another small spine on the left side, which is almost inconspicuous.

Female Genitalia. The sterigma forms a single semi-cylindrical plate (Fig. 112). In ventral view, its trapezoidal aspect can be observed, where it has at its center an area with little sclerotization next to a glandular organ which is adhered to its anterior margin, whose function is yet unknown. It is directly coupled to the eighth tergum, which is well developed, semi-cylindrical and posteriorly shelters the anal papilla. The ostium bursa appears median-ventrally sheltered in a ventral concavity of the postvaginal lamella.

The bursa presents a terminal dilatation, anteriorly to the vertex found in the middle of its length (Fig. 116). The spermatophore is composed of a globular terminal dilatation (sheltered by the dilatation in the body of the bursa), next to a thin and cylindrical anterior projection. The spermatophore is distinctly less sclerotized than that of the previous species. Anal papillae, which are slightly reduced in volume, present the same appearance as the previous species, provided with thin posterior apophyses that are distinctly longer than the ones found in *Urbanus teleus*.

Synapte silius (Latreille, [1824])

Cervix and Prothorax. The dorsal-ventral distance of the cervix is proportionally a little smaller than the one observed in the previous species (Fig. 4). The presence of the cervical organ was not observed.

The dorsal plate of the cordiform pronotum presents sclerotization on the lateral-dorsal margin, continuing ventrally and gradually disappearing (Fig. 8). The posterior margin of the extension has a median recess providing the structure with a bifid appearance. The apophysis has a short base and branches are slightly longer than in the other species. The posterior band of the parapatagia is well sclerotized, unlike the trochantin, which form a triangle-shaped structure located dorsally on the coxa (Fig. 65). The small thin bars located on the posterior edges of the pronotal dorsal membrane are laterally dislocated to the lateral ends of the membrane.

Mesothorax. It is of intermediate size, having proportions similar to those of *Urbanus teleus*, though without oblique sulci (Fig. 16). Among the notal wing processes, the most evident is the anterior, which is ventrally projected, forming a hook on the apex, with the end turned posteriorly. The other processes are similar to those in previously described Pyrginae (Fig. 12).

Ventrally, the subtegula II presents a shape similar to that of the *Pyrrhopyge charybdis charybdis*. However, beside the basalare it is reduced to a small oval sclerite. The subalare sclerites are narrow on its median region, and their extensions are not very prominent. The tegula is similar to *Urbanus teleus*, though presenting an irregular ventral orifice and a reduced membranous area (Fig. 24).

The anepisternum II presents, besides an anepisternal suture II as long as in *Pyrrhopyge charybdis charybdis* and *Pyrgus orcus*, another inconspicuous dorsal-ventral line that crosses the posterior half of the sclerite (Fig. 20 and 53). The coxal suture II ventrally separates the entire katepisternum II from the basisternum II. Likewise, the marginopleural suture reaches the precoxal suture II and separates a small sclerite ventral to the katepisternum II (Fig. 12). The ventral articulations of the coxa II are inserted on the median crest between the coxae, posteriorly on the discrimen II. Epimeron II is similar to the one in *Pyrrhopyge charybdis charybdis* (Fig. 20).

Metathorax. The marginopleural suture III, though incomplete, is longer than those in the Pyrginae observed herein, leaving just a small ventral portion still blended to the katepisternum III (Fig. 28). In the epimeron III, the same dorsal recess found in *Urbanus teleus* is also visible in all the studied specimens.

Legs. The femur I is longer, surpassing twice the length of the tibia I (Fig. 32). The basicostal suture III is developed, oblique and contiguous to the pleural suture III. The meron II presents a differentiated

triangular dorsal sclerite, as observed in the Pyrginae (Fig. 20). The pre-tarsus is similar to that of *Pyrrhopyge charybdis* (Fig. 61).

Wings. Wingspan pattern similar to that of *Pyrgus orcus*, measuring approximately 27 mm. Venation is similar to that of *Pyrgus orcus* (Fig. 36). The discal cell is of proportional size, the dcs vein is small, there is no sexual dimorphism along the insertion distance of the M_1 in relation to R_{4+5} and the 3A veins are equally reduced, provided with extensions and sexually differentiated distances, similar to the previous species. The M_2 vein is closer to the M_3 than to M_1 at the base, and the dcm, dci, and M_2 veins are not well delimited in both wings. Males do not present a costal crease.

Long scales are located on the costal margin the hind wings (Fig. 49). The same humeral vein and slim M_2, present in *Pyrgus orcus,* are observed. There are no significant sexual differences in the extension of the m-cu.

Abdomen. The tergal lobe is weakly sclerotized and distinguished in males because of its great development (Fig. 72 and 73). The prespiracular bar is similar to those of the Pyrginae studied here, distinguishable from the first sternum by a clear suture. Conversely, the postspiracular bar is strongly projected towards the ventral area, even though it does not meet the second sternum either. The tergopleural bar is similar to those of *Urbanus teleus* and *Pyrgus orcus*. The first tergum is as developed as it is in *Pyrgus orcus* while the first sternum does not present any keel-shaped ventral prominences. The last pregenital segment does not present either membranous recesses or punctuation for bristle insertion. The last tergum is rectangular with an arched posterior edge in females, along with a small semicircular recess (Fig. 86 and 87). The sterna are laterally reduced, with sinuous lateral edges in males and parallel edges in females (Fig. 88 and 89).

Male Genitalia. The tegument is reduced to a small dorsal plate, flattened dorsal-ventrally and semi-oval in shape (in dorsal view). The uncus is U-shaped, presenting widely separated thin arms, whose basal area is covered by a thick cluster of bristles located on its anterior margin (Fig. 101). Ventrally, the membranous area has the shape of a long vase, where another pair of sinuous plates can be seen laterally that are adhered to the arms of the gnathos, which are slightly sclerotized. The gnathos is distinctly projected posteriorly, allowing its visualization in dorsal view, and is made up of a pair of tubular arms with a rounded apex. The fultura inferior is U-shaped, bigger than in *Pyrgus orcus*, due to the more developed anterior projections (Fig. 105).

The saccus is not dorsally projected, and is reduced to a small anterior dilatation, measuring ¼ the length of the ninth segment (Fig. 96). The dorsal projections of the saccus are blended to the ventral ones of the tegumen. The valva is directly articulated to the saccus, without any specific articulation insertion, forming a single lobular arm, posteriorly rounded. The harpe has a sinuous dorsal margin, and the apical margin is provided with a cluster of bristles as in the other species (Fig. 97). The costa is almost imperceptible in lateral view at the base of the valva, being similar to a thin edge near the base of insertion of the valva. However, a partially superimposed tooth posteriorly to the costa is directed towards the margin of the harpe. The sacculus is represented by just a small shortened basal crease, reaching around one third of the height of the valva.

The aedoeagus is small in extension and wide in thickness (Fig. 109). Its truncated ends display a rectangular appearance, instead of the baton shape observed in the other species. Additionally, there is a membranous dorsal spot which is triangular and elongated on the dorsal and distal ends. The vesica is not reversed on the dissected individuals and a helicoidal cornuti full of small thorns all over its surface, can be seen internally.

Female Genitalia. The whole genitalia in *Synapte silius* clearly does not follows the direction of body axis like in the other species observed herein. In this species, the genitalia is directed ventrally, assuming a 45° with body longitudinal axes, as evidenced by the position of anal papillae, in comparison to the last tergum (Fig. 113).

The sterigma is absent due to the lack of sclerotization of the postvaginal lamella. The antevaginal lamella, which is quite evident, is formed by two rectangular plates that are ventrally united by a membrane (Fig. 117). Posteriorly, in ventral view, a membranous area between the anal papillae is observed which is provided with sclerotized areas that are not seen in the other species.

The anal papillae are higher than wide, and present the same lack of sclerotization of the anterior portion, which is also present in *Urbanus teleus*. The anterior apophyses are inserted anteriorly, and are shorter than those in *Urbanus teleus*, also presenting a triangular dilatation next to their insertion.

Subsequent to the ostium bursa, there is a short cylinder which is slightly sclerotized, presenting striation on its lateral margins. Posteriorly, the rest of the duct of the bursa is entirely membranous like the body itself, and gradually dilating towards a globular apex. The spermatophore was not found in any of the specimens observed.

Discussion

Cervix and Prothorax. The cervical sclerite is very similar in the species examined (Fig. 1 to 4) and also similar to those found in *Astraptes fulgerator* (Walch, 1775) (Pyrginae, Eudamini) and *Sarbia xanthippe* (Latreille, 1824) (Pyrrhopyginae) (Niculescu 1978). The ventral projection, though developed, is not blended to the median area as in Papilionidae (Ehrlich 1958b; Srivastava 1961) or Sphingidae (Madden 1944). The cervical organ, described by Ehrlich (1958a), should be object of detailed studies regarding its variability and function. Its greater development in *Pyrrhopyge charybdis charybdis* contrasts with its total absence in *Synapte silius*, or its lesser development in the Pyrginae studied, and in those described by Ehrlich (1960). Papilionoidea also present a large variation, from greater development (Ehrlich 1958b) to considerable reduction (Sorensen 1980). Kristensen (2003) refers to the organ as "hair plates", and says it is present in different Lepidopteran groups, under different shapes, probably being a homoplastic condition for the order.

The pronotum, a character of significant taxonomic importance and that varies on a large scale, can be visualized in different shapes both in Lepidopteran families (Shultz 1914; Kristensen 2003) and in Hesperiidae genera (Niculescu 1978). The dorsal plate is not often illustrated by authors due to its visualization being partially obstructed by the prescutum II, where it articulates.

Niculescu (1978) emphasizes the great variability of shapes presented by the dorsal plate of the pronotum, a structure that is seldom entirely illustrated and described, due to its difficult visualization and by the large part hidden under the prescutum II. The distinct spot patterns (Fig. 5 to 8) differ in all the species illustrated by the quoted author, suggesting a variation greater than the one proposed by him. The few similarities do not coincide with the *a priori* phylogenetic positioning within the family (De Jong et al. 1996; Ackery et al. 1999).

The pair of patagia were also similar (Fig. 1 to 4), though Ehrlich (1958b) described a series of modifications in Papilionoidea. In contrast, the parapatagia varied in their degree of sclerotization of both bands, in the anterior band of *Urbanus teleus* and in the posterior band of *Synapte silius*. Together with the Charaxinae (Ehrlich 1958b), the Hesperiidae are the only butterflies that present this structure, along with some cases in the Tineidae, Yponomeutidae, Zygaenoidea, and Bombycoidea (Schultz 1914), and their differing degrees of sclerotization suggests that its disappearance may be an intermediate character for the majority of the Papilionoidea lineages.

The thin bars (Fig. 5 to 8), which are sclerotized, parallel and posterior to the parapatagia, should undergo a more investigative analysis in order to discover their presence in other groups and infer their real taxonomic importance. In general, the shapes of the lateral plate of the episternum I and the preepisternum I, along with their articulations, vary at a small scale, and are mostly devoid of informative characters for their differentiation. Also, the position of the and degree of sclerotization of the lateral-posterior portion of the episternum I should be better explored in order to contribute to the understanding of the modifications in such structure, which might be interpreted as a reduction of the epimeron or the pleural suture.

The trochantin I (Fig. 9-12 and 62 to 65), which is always present, varied little in shape, even though it is quadrangular in *Urbanus teleus* and triangular in the other species. Its distinct sclerotization can be interpreted as the possible beginning of the disappearance of this structure, as observed in the great majority of Lepidoptera (Matsuda 1970), though several species still need to be investigated in order to propose such an explanation.

The spina I had already been mentioned as a potential character for the identification of Hesperiidae genera (Shepard 1930). The author reports its differences, and even exemplifies cases such as its greater development in Eudamini genera, when compared to the Pyrgini. The variation of the spina I can be intimately linked to the genus level (Shepard, 1930). Of the species examined, (Fig. 9 to 12), *Pyrgus orcus* presented the greatest development, contrary to the observations by Shepard (1930). In the other species, small variations are found in the apical angle and shape of the structure.

Mesothorax. The developed notum of this tagma presented small size modifications (Fig. 13 to 16), such as its narrowing in *Pyrgus orcus*, or the presence of sulci oblique to the mesoscutal line in *Urbanus teleus* and *Pyrrhopyge charybdis charybdis*.

Unlike the majority of butterflies, the prescutum II is not visible in lateral view, due in great part to its concave anterior surface. Among the species studied, no significant variations of this structure were observed. The scutum II and scutellum II are also characterized in this way. In Papilionoidea, Ehrlich (1958b) found differences in the angles formed by the scutoscutellar suture II, similar to that observed in this study. However, the use of such a character can face difficulties because of the presence of several intermediate states in the angulation of the structure. Ehrlich (1958b) also notes that it is not useful for the classification of larger groups.

The anterior notal process assumes different formats (Fig. 17 to 20) which might be related to the articulation with the cervical sclerites, and consequently with flight behavior. However, the difficulty to visualize its structure, as its presence and angulation are hidden and changed due to the axillary sclerites, limit its taxonomic use. The development of the median notal process, beside being very similar to that in *Epargyreus clarus* (Pyrginae, Eudamini) illustrated by Ehrlich (1960), is also similar to examples from other Lepidopteran families, such as in the Pyralidae (Camargo 1980); Sphingidae (Madden 1944); Saturniidae (Michener 1952); Lycaenidae (Sorensen 1980); Nymphalidae (Ehrlich 1958a; Bizarro 2003a) or even in primitive families such as the Opostegidae (Kristensen 2003). Other studies, which do not make such a conformation evident, like in the Tortricidae (Freeman 1947), Nymphalidae, Morphinae (Bilotta 1994a), and in the Saturniidae (Camargo et al. 2005), can provide important subsidies for the differentiation of this character, so widely distributed in Lepidoptera. On the other hand, the difficult visualization of this structure, as indicated in this study, might provide false evidence, making it necessary to repeat these observations. The same restriction applies to the other sclerites appearing on the pleural membrane, such as the subtegula, the basalare II and the subalare II.

The elongated shapes of the posterior portions of the tegulae, surpassing the insertion of the wings, confirm a characteristic of the lineages derived within the Ditrysia (Kristensen 2003). Additionally, it is possible to emphasize the differences, which are also significant, in the basal portion where the tegula is inserted (Fig. 21 to 24). However, for the posterior face, which is seldom illustrated, the median location of the insertion orifice seems to differentiate the majority of the butterflies, where it is located adjacent to the margin (Kristensen 2003). *Pyrrhopyge charybdis charybdis* was the only species to present a suture on the internal face of the tegula.

Mentioned as one of the main characteristics of the Hesperiidae (Niculescu 1970; Ehrlich 1960), the presence of a developed anepisternum II, partially blended to the katepisternum II and ventrally limited by an anepisternal suture II, differentiates them from great part of the Papilionoidea (Ehrlich 1958b). According to Kristensen (2003), the reduction of this sclerite prevails in Papilionoidea, though some species of Hesperiidae and Papilionidae might develop it independently. In the present study, there were no significant variations in its development (Fig. 50 to 53), except for the extension of the anepisternal suture, which is reduced in *Urbanus teleus* and in *Epargyreus clarus*, as illustrated by Ehrlich (1960).

The sutures located between the katepisternum II, the basisternum II, and the paraepisternum II (Fig. 9 to 12) vary in all species. The configuration of the different shapes of the precoxal suture II has a great potential for use in the classification of Hesperiidae. The different degrees of this line, from straight, to curved, or complete and incomplete, might provide supplementary information after comparison with the other species in the group. Next to the coxa, the precoxal suture II is complete in *Pyrrhopyge charybdis* and *Synapte silius*, or presents small discontinuities next to the pleural suture II (*Pyrgus orcus*) or to the sternopleural suture II (*Urbanus teleus*). Once again, the similarity of *Urbanus teleus* with *Epargyreus clarus* is evident.

Among the Hesperiidae, the presence of a differentiated preepisternum II can still be contested. Even if it is present, the line separating this structure is not well delineated, at a certain point reaching entirely inconspicuous portions. Through information collected in the present study, and from the illustrations done by Ehrlich (1958b) and Sorensen (1980), it is possible to infer the disappearance of this structure in certain Lepidoptera species. Kristensen (2003) states that its presence is constant in basal forms of the order, and such a statement clashes with the one proposed by Matsuda (1970), who believes there is a secondary development of this structure in Lepidoptera, denominated paraepisternum II.

After the removal of the coxae II it is possible to ventrally observe the point of coxal ventral articulation II, usually located posteriorly to the basisternum II. However, *Pyrrhopyge charybdis* presents this structure interiorly dislocated to the base of the furca II, while in *Pyrgus orcus* it is almost located next to the basisternum II. In contrast, the illustrations made using Scanning Electron Microscopy show the small depression formed by the coxal-pleural articulation (Fig. 54 to 57), considered by other authors as a differentiated sclerite, usually denominated basicoxite.

The epimeron II (Fig. 17 to 20) does not vary in form among the species studied. However, the presence of the preepimeral suture II (Fig. 19) in *Pyrgus orcus*, might provide new information about the Pyrgini, if studied further and compared with the other species of the tribe. This suture had not previously been illustrated for the Hesperiidae. Its presence in the Zygaenoidea, the Pyraloidea, or in the Sphingidae, Noctuidae and Geometridae (Shepard 1930), with different shapes, suggests an independent transformation of this structure within the order. The fusion of the dorsal-posterior portion of the epimeron II with the arms of the furca II is considered as an important synapomorphy of Lepidoptera + Trichoptera (Kristensen 2003). The same author considers that its study deserves further observation though he characterizes its presence as still developed in non-Glossata lineages. In the species examined, this bridge is strong and developed.

Metathorax. Dorsal-laterally, there are no significant structural modifications. The position of the subalare III, circled by membranes on all sides, is highly susceptible to the methods used in the preparation of the specimens, which ends up deforming the membranous portions of the insect.

Changes occur in the pleural sclerites regarding the location of the internal crest and extension of the marginopleural suture, both of which are located in the katepisternum II (Fig. 25 to 28). The anepisternum III, which is practically uniform, hides the second thoracic spiracle from visualization, which, even with the removal of the sclerite, was not observed in any of the specimens.

The Pyrginae analyzed herein presented a strong similarity in this tagma, which stands out by the presence of the anterior projection of the paraepisternum III, not seen in the other species. *Epargyreus clarus* also shares the same characteristics (Ehrlich 1960). Another peculiar characteristic refers to the presence of a hook-shaped dorsal membranous recess in the epimeron III of *Urbanus teleus* and *Synapte silius*, located near the region where some of the tympanic organs of certain Lepidoptera are found. Its internal examination might detect structures that are yet unknown in the family. The same recess was also observed in *Epargyreus clarus* by Ehrlich (1960).

Barth (1960) describes in *Pyrgus*, as well as in a several Pyrgini genera, the presence of a glandular pouch in the metathorax associated with a hair tuft on the tibiae, found in *Pyrgus orcus* herein (Fig. 27). According to some general Hesperiidae studies (Lindsey 1921; Evans 1952, 1953), the presence of such structures is quite variable even among species of the same genus, and is thought to be informative to diagnose some genera. Similar organs were also identified in species of Pyrrhopygini, Oxynetrini, Passovini (Pyrrhopyginae), Eudamini (Pyrginae) as mentioned by Barth (1960), but the homology of this character still remains to be studied. According to the author, similar glands are not observed in other Lepidoptera.

Legs. Unlike part of the Papilionoidea, none of the observed species presented signals of reduction in any of the segments of the legs (Fig. 29 to 32). Additionally, Hesperiidae also lacks a coxal sulcus or internal crest in the coxa I, a character absent in *Glaucopsyche lygdamus* (Lycaenidae), although present in *Papilio demoleus* Linnaeus, 1758 (Srivastava 1961) and in *Parides anchises nephalion* (Godart, 1819) (pers. obs.). In all the species examined, a uniform bar presenting greater sclerotization and being distinguished by a line or small crease was found next to the articulation with trochantin I, which has not been mentioned in other morphological studies.

In all four species, the femur decreases in size from the anterior to the last segment. In contrast, the tibia progressively increases in size, except in *Pyrgus orcus* and *Synapte silius* which remains the same size in the meso- and metathorax. Ehrlich (1960) observed the inversion on the size of mesothoracic femurs, in detriment to the metathoracic ones, bigger and smaller than their respective tibias, a pattern that is corroborated in this study. The tarsi are longer in the metathorax, and shorter in the mesothorax.

Some of the structures seem to be apparently homogenous among the species, such as the trochantin, the presence of pairs of tibial spurs and the epiphyses; the latter deserving further studies due to its close relationship with several characteristic antennae in the Hesperiidae (Fox 1976).

The absence of spines and scales is constant on the ventral face of the last prothoracic tarsomere, as well as their presence is constant on the meso- and metathoracic legs. The apical sensitive bristles, on the other hand, was represented by one pair in all species except for *Urbanus teleus*, which together with *Epargyreus clarus* (Ehrlich 1960), presents two pairs of sensitive bristles. Bilotta (1994a) illustrates three pairs of these bristles in some species of Morphinae (Nymphalidae).

The coxae II and III are subdivided into the eucoxa II and III (anteriorly) and the meron II and III (posteriorly) by the basicostal sutures II and III, respectively, which are slightly curved and dorsally contiguous to the pleural sutures II and III (Fig. 17 to 20, 25 to 28). The pterothoracic coxae form a conic structure projected from the abdomen, a little shorter than the anterior coxa. In contrast, the tibiae II and III are longer on the meso and metathoracic legs, when compared to the femurs, and possess spurs instead of epiphyses as in the prothoracic legs: having two apical spurs on the mesothoracic pair; and two apical spurs, plus two subapical ones, on the metathoracic pair. The asymmetry of the spurs, the internal one being 2/3 longer than the external one (illustrations given herein does not allow such precise observation), might occur because of a behavior that has yet to been described. The meron III presents a subdivision delineated by a longitudinal suture, which is absent on the anterior segment, forming a triangular dorsal area, with an also triangular membranous ventral portion.

The pretarsus, which is similar in all the legs and almost all the species (Fig. 58 to 61), presents a trifurcated arolium in *Pyrgus orcus*, and a modified bifurcated arolium in the other species. However, its visualization may be difficult due to the certain transparency of its structure, as well as by its diminutive size, in *Pyrgus orcus*. The tarsal claw, usually presenting a truncated ventral projection, is sharpened as a spine in *Pyrgus orcus*, although partially covered by the arolium. In the other species, the pretarsal structures are uniform.

Wings. The wingspan of female Lepidoptera is traditionally recognized to be, in general, bigger than that of the males (i.e. Austin and Mielke 2008), which constitutes a sexually dimorphic character widely used for gender differentiation. However, the sizes of *Synapte silius* and *Pyrgus orcus*, with males being slightly bigger than females, contradict this pattern, and there is a lack of research on the factors that influence such differences.

Likewise, the presence of the costal vein (Fig. 39) reveals itself to be a character still little explored within the Lepidoptera and, therefore, difficult to compare. Several authors do not illustrate it as a true vein (Ehrlich 1958a; Sorensen 1980; Bilotta 1994a; Bizarro et al. 2003a; Camargo et al. 2005), though Ehrlich mentions the presence of a costal sclerite (1958a), and later (1960) illustrates it on the costal margin of *Epargyreus clarus*, both on the fore and the hind wings. However, the author never mentions its presence, and his illustrations corroborate those presented in this study. Madden (1944) and Freeman (1947) illustrate its presence on the forewing, but do not discuss its presence, structure or taxonomical importance either.

The occurrence of the costal vein is so characteristic that it is responsible for the formation of the costal crease, a tegumental crease on the costal margin in males of several Hesperiidae, (A. Müller 1878) (Fig. 37, 38). *Pyrgus orcus* was the only species to present such a character. Though Evans (1952) considers its presence common in the *Urbanus* "group" (subdivisions adopted in his study), there is a group of species listed by the same author that do not have a costal crease, among them *Urbanus teleus*. The same author also alerts to its absence in all the Hesperiinae. Brock (1971) attributes the "primitive" venation of Hesperiidae to the occurrence of the M1 taking root in the R5, corroborating the patterns found here. However, the transversal connecting vein between R5 and M1 (dcs) significantly varied (Fig. 33 to 36), either in size between sexes of *Pyrrhopyge charybdis charybdis* and *Urbanus teleus,* or being weak or even difficult to visualize in the other species.

The dcm and dci veins in the fore wings and hind wings, as well as the M2, were difficult to visualize in all species studied herein (Fig. 40 and 41). It is important to emphasize that their observation can be highly influenced by the preparation methodology, due to its complete disappearance after moderate exposure to sodium hypochlorite.

The size of the discal cell is also an important character in the classification of Hesperiidae. In *Pyrrhopyge charybdis charybdis* and all the Pyrrhopyginae (Evans, 1951) its extension exceeds the length of the anal margin or 2/3 of the costal margin. Similarly, both tribes of Pyrginae (Pyrgini and Eudamini) are diagnosed by the size of discal cell (Evans, 1952), being around half the length of the costal margin in Pyrgini and near two thirds in Eudamini, or still greater than or equal to the anal margin in the Pyrgini

and smaller in Eudamini. The species described in the present study corroborate this assumption, furthermore no exceptions were described in the literature about this characteristic.

Urbanus teleus was the only species to present a recurring M inside the discal cell (Fig. 41). The presence of this structure, also detected by Ehrlich (1960) in *Epargyreus clarus*, is an important character to be observed amongst the Eudamini, especially in the *Urbanus* "group." The position of M_2 next to the M_1 reflects a differential characteristic for the Pyrginae studied herein. *Pyrrhopyge charybdis charybdis* is distinguished, by this characteristic, from *Synapte silius* by having a dcm a little larger than the dci, reaching twice the extension of the dci in *Synapte silius*.

According to Ackery et al. (1999), the Hesperiinae possesses a characteristic M_2 vein on forewing, which is directed towards the M_3. Even though such a character has been confirmed in *Synapte silius*, a similar manifestation is observed in *Pyrrhopyge charybdis charybdis*, a fact that dismisses the usage of this character as an autapomorphy for the Hesperiinae.

The length of the 3A is especially important because it characterizes interspecific and/or intersexual differences. In *Pyrrhopyge charybdis charybdis* and *Urbanus teleus*, where there is no significant sexual dimorphism, the length is around 1 and 1.5 times the distance from the cubital to its first bifurcation, respectively. In *Pyrgus orcus* this ratio is 3 and 4.5 times in males and females, and in *Synapte silius* it is 2.5 and 3.5 times, respectively.

In the hind wings, the most significant character was the absence of the M_2 in *Pyrrhopyge charybdis charybdis* and *Urbanus teleus*, which was also observed in the study by Ehrlich (1960) with *Epargyreus clarus*. In all these species, there is no clear differentiation of dcm and dci, despite the curvature of each one in the other species studied. In the hind wings of *Pyrrhopyge charybdis charybdis*, *Urbanus teleus*, and *Pyrgus orcus*, there is yet another secondary sexual character, the m-cu is twice as long in females than in males.

The hind wings present more round angles and a decreased number of longitudinal veins, to nine. The costal vein provides structure to the humeral angle, stretching towards the bifurcation of Sc and R. This area, which is highly developed in Hesperiidae and partially surrounded by the back, was mentioned by Comstock (1918) as originating from a coupling mechanism that replaces the frenulum and the retinaculum. According to the author, the superposition of the wings over an specific area, in itself, should be capable to synchronize the wing flapping. The strongly developed humeral angle observed in all studied species (Fig. 42 to 49) supports this idea, even though there are no such observations of *Euschemon* (Hesperiidae, Euschemoninae), the only genus among butterflies to possess a frenulum. Additionally, the differentiated scales on the contact zone between the wings deserves more detailed studies, once it interacts directly with wing coupling system in this group. *Pyrgus orcus* and *Synapte silius* shows elongated scales on hindwing while *Pyrrhopyge charybdis* and *Urbanus teleus* have a spot of opaque scales on both sides where wings have contact.

Abdomen. With the lack of sensorial organs or odoriferous glands, the usage of taxonomic characters applied to the tagma are limited, due mainly to the great difficulty in viewing the structures present under the thick coverage of scales that completely cover its surface. Watson (1893) and Evans (1951-1955) hardly mention abdominal characters in their classification and/or identification key.

The presence of the prespiracular bar, separated in *Pyrrhopyge charybdis charybdis*, *Pyrgus orcus*, and *Synapte silius*, or blended to the first abdominal sternum in *Urbanus teleus*, might suggest a probable origin and modification of such a structure. Ehrlich (1958b) reports the presence of such a structure in all Papilionoidea, except for Pieridae, although he does not mention its condition for each taxa. Bilotta (1994b) does not mention the presence of this structure in Morphinae (Nymphalidae), though in *Caligo beltrao* (Illiger, 1801) (Nymphalidae, Brassolinae) there is a developed and projected apophysis on the first sternum that was thus denominated by Casagrande (1979b). There are also strong modifications on the first abdominal segments due to mimicry or oviposition (Bizarro et al. 2003b) that were not observed in species studied, although they may contribute substantially to studies of comparative morphology.

Likewise, Ehrlich (1958b) attributes the presence of the complete postspiracular bar as a typical characteristic in some genera of Nymphalidae, in contrast with its reduction or total absence in Papilionidae, Lycaenidae, Riodinidae and other Nymphalidae. The presence of this character in all the species studied herein reveals the great amplitude of manifestations and levels of development that this structure might represent. However, the extreme reduction of the postspiracular bar, added to the fusion of the prespiracular bar to the sternal apodeme, shared by *Epargyreus clarus* (Cramer, 1775) (Eudamini,

Pyrginae, Hesperiidae) (Ehrlich 1960) and *Urbanus teleus*, might serve in the future for systematic inferences among Eudamini groups, and deserves comparative studies with other species.

Ackery et al. (1999) proposed the use of the reduced format of the first abdominal tergum as an autapomorphy of Pyrrhopyginae, which was corroborated within the group, in the cladistic study by Mielke (2001), and is also confirmed herein. However, its development, evident in *Pyrgus orcus* and *Synapte silius* specimens, is not mentioned in the literature and therefore deserves further examination. No membranous spot was found on the tergum of the studied Hesperiidae, in contrast to its great variability in some groups of Papilionoidea (Ehrlich 1958b).

The use of the size and/or development of the tergal lobe might still be, *a priori*, hindered by its difficulty in being visualized and extreme fragility, due to its low level of sclerotization and its location between membranes. It is possible that this structure is related to the protection of the first abdominal spiracle. The constant presence of the tergopleural bar does not offer differential information among lineages of Papilionoidea and Hesperioidea.

Male Genitalia. Obviously, the great variation in forms of the male genitalia, which is already used in species identification, cannot be observed in this study. Therefore, a great part of this discussion is confined to comparisons with genitalia described in closely related groups, which allows a better comprehension of its development.

There is a wide range of modifications in the tegumen that might be presented within this structure, besides the presence or absence of strong and well developed apophyses, as in *Pyrrhopyge charybdis charybdis*. *Synapte silus* was the only one to present a considerable reduction of this structure, besides the dorsal-ventral flattening, forming a bulging pattern which differentiates it from the other species. The length of this structure differentiates both *Urbanus teleus* and *Pyrgus orcus* from *Pyrrhopyge charybdis charybdis*. The uncus and the gnathos have unique shapes, which are practically distinct in each species observed within the Hesperiidae (see Evans 1951, 1952, 1953 and 1955). However, the membranous opening of the uncus, which is present in ventral view and usually omitted in illustrations, is highly modified in all the species studied herein.

The uncus, which is bilobed in all four species, presents its two posterior projections almost blended together in *Pyrgus orcus*, next to each other in *Pyrrhopyge charybdis* and *Urbanus teleus*, or separated from each other in *Synapte silius*. The ends of these projections can be blunt (*Pyrrhopyge charybdis charybdis* and *Urbanus teleus*), sharpened (*Pyrgus orcus* and *Synapte silius*), or semi-cordiform (*Pyrgus orcus*), with or without bristles on the dorsal surface (Fig. 98 to 101).

All shapes of the gnathos, illustrated in Pyrrhopyginae (Mielke 2001), may yet become more distinct when the entire family is studied. Among the triangular, tubular, and spatula-like shapes observed herein, there also other shapes which were not mentioned but provide fundamental evidence for the distinction of groups such as the Pyrrhopyginae (Mielke 2001) and many others that have yet to be explored. De Jong (1972) describes a distinctively differentiated gnathos from those of *Pyrgus orcus* in some palearctic species of *Pyrgus* Hübner [1819], along with several variations of the other sclerites in the genitalia. The protraction of the gnathos, expressed in *Synapte silius*, is a fundamental character for the identification of the species belonging to the same genus (Evans 1955).

The presence of the fultura superior in *Pyrgus orcus* (Fig. 100) contrasts with its absence in most Neotropical (Austin and Warren 2001) and all Palearctic species (De Jong 1972). From the illustrations available in Austin and Warren (2001) it is possible to indicate its presence only in *Pyrgus oileus* (Linnaeus, 1767), *Pyrgus philetas* (Edwards, 1881), and *Pyrgus brenda* (Evans, 1942).

Pyrrhopyge charybdis charybdis presented a distinguish fultura inferior from all the other species. The fultura inferior in this species, which usually is U- or V-shaped, is developed in lobular shape, being confused with the manica, which apparently is more keratinized and presents tegumental grooves all over its length. Its shape is used in the identification of Pyrrhopyginae tribes (Mielke 2001). In contrast to that illustrated for *Pyrgus orcus* by Austin & Warren (2001), the fultura inferior in *Pyrgus orcus* is distinctly shorter, does not present lateral extensions, and is concave in the middle, presenting a V-shape (Fig. 104) and not a triangular appearance, as illustrated by the authors.

The shape of the saccus, different in the four species, seems to vary substantially regarding its anterior and dorsal development. In *Pyrrhopyge charybdis* it is unique with respect to its dorsal development (Fig. 21), while in *Pyrgus orcus* it is distinctly long, thin and anteriorly projected (Fig. 25), unlike the other species in which it is short. Mielke (2001) used its anterior development to hypothesize a

phylogenetic relationship amongst the Oxynetrini, when compared to the other Pyrrhopyginae. Its extension reaches half the length of the ninth abdominal segment in *Pyrrhopyge charybdis charybdis*, contrary to *Urbanus teleus* and *Synpate silius* which do not surpass one quarter of the same distance. However, it is possible to notice variations of this structure among species of a single genus (Burns et al. 2007), such as *Polyctor* Evans, 1953 (Pyrgini, Pyrginae, Hesperiidae), which might limit its use for the distinction of larger groups among the other Hesperiidae.

The constant presence of completely blended ventral and dorsal projections, of the tegument and saccus, respectively, forms a ring adhered to the inter-segmental membrane which is responsible for the fixation of the genitalia to the rest of the abdomen. These structures were not observed either separated or articulated to any degree. A thickening of the ventral projection of the tegument, present in *Urbanus teleus* (Fig. 92) and shared with *Epargyreus clarus* (Ehrlich 1960), might suggest a close relationship between the two genera, already indicated by Evans (1952) as belonging to the same "Urbanus subgroup" amongst the Eudamini.

Usually considered as the main structure used for the identification of the Hesperiidae (see Evans 1951, 1952, 1953, and 1955), the valva presented herein indicate too specific modifications for comparison amongst taxonomical hierarchical levels above species or genus (Fig. 90 to 97).

The harpe can be enlarged, filling almost half of the internal face of the valva as in *Pyrrhopyge charybdis charybdis*; or smaller about one fifth of its length, as in *Pyrgus orcus* studied herein. Or it can even be difficult to distinguish from the sacculus, as in *Synapte silius*. Its taxonomic use should be more precisely evaluated at specific levels, due to the great variability of the character found in any of the four species.

The presence of the ampulla, indicated as a common character in Hesperiidae (Ogata 1957), and especially well developed in *Pyrgus* (De Jong 1972), was not observed in any of the species studied herein, not even in *Pyrgus orcu*s. This suggests that this character might easily separate the Palearctic from New World species, where its presence is less outstanding or almost imperceptible (Austin and Warren 2001). However, the homology of this structure, which was originally described in Noctuidae, is difficult to determine. For example, when compared to species such as *Pyrrhopyge charybdis charybdis*, in which a differentiated projection occurs, though directed in the opposite direction than that proposed by Ogata (1957), i.e. anterior projection of the harpe). Sibatani et al. (1954) suggest that in some forms of Hesperiidae, the ampulla and the harpe are blended to the terminal portion of the valva, making its presence vestigial or imperceptible. Examining several species of Hesperiidae, it is indeed common to find different types of dorsal projections originating from the costa and harpe (see Evans 1951, 1952, 1953, and 1955). However, establishing an assumption that all those projections are homologous with the ampulla in Noctuidae can lead to a serious misleading interpretation of genitalia structures. The costa can be laterally (*Pyrrhopyge charybdis charybdis*) or dorsally, represented by a narrow edge (*Synapte silius*), a small triangular crease (*Urbanus teleus*), or well developed and possessing long bristles on is ventral end (*Pyrgus orcus*).

The internal creases of the sacculus vary in development and shape, reaching half the height of the valva in *Pyrrhopyge charybdis charybdis*, a third of its height in *Urbanus teleus*, or less than one fifth, very reduced and having a sinuous margin in *Pyrgus orcus* and *Synpate silius*. A large part of the species of the genus *Synapte* is differentiated by the shape of the sacculus and the back (including the dorsal-posterior spine) (Evans 1955).

Similar in all the species studied, the aedoeagus is tubular and has proportionally differentiated sizes, both in length and diameter (Fig. 106 to 109). Several Hesperiinae species, sometimes phylogenetically distant, present an extremely elongated or robust aedoeagus, a structure that probably has strictly specific level characteristics. A variation in the shape and development of the aedoeagus' coecum is visible in all the species studied herein, and might be a good character for their identification. Only *Synapte silius* presented this structure as reduced, while the extension in the other species varies in thickness, length and curvature.

Considering the extensive illustration presented by Oiticica (1946), the globular or oval ejaculatory bulbs in the Hesperiidae studied here differ from a large part of the species presented by him, usually having slim and tubular ducts or presenting dilatations of other shapes, as in the Pieridae, Nymphalidae, Castnidae, and Sphingidae species mentioned by the author. Bizarro et al. (2003b) and C. Mielke et al. (2004) illustrate the ejaculatory bulb as a reduced and rectangular membrane. Other authors do not even

illustrate its presence (Freeman 1947; Ehrlich 1958a, 1960; Sorensen 1980; Bilotta 1994b). The study that presents the most similar structure is by Casagrande (1979b) with *Caligo beltrao*, however it differs from the tubular form in *Brassolis astyra* (Godart, 1819) illustrated by Oiticica (1946).

Posteriorly, the presence of a long and hard spine on the right side of the aedoeagus separates *Pyrgus orcus* from the other species. *Pyrrhopyge charybdis charybdis* also presents a crease on the same side, however, it is replaced by a cluster of small lateral-ventral spines (Fig. 38). A membranous spot was observed on the distal-ventral surface in *Pyrrhopyge charybdis* and distal-dorsal surface in *Synapte silius*, which was not found on the other species. *Pyrrhopyge charybdis charybis* also presents a curvature, but develops it on the median portion, differently from the posterior one in *Urbanus teleus* and *Pyrgus orcus*.

Urbanus teleus and *Synapte silius* presented cornuti, observed sometimes through transparency, once this structure lays inside the aedoeagus when in resting position. For the same reason, it was not possible to compare this structure, even though its great taxonomic importance is assumed.

Female Genitalia. The differentiated eighth tergite is directly connected to the genitalia, the main reason for its inclusion in this section. However, its shape has never been included in systematic studies in Hesperiidae, despite its great variability. In *Pyrrhopyge charybdis charybdis*, its shape is reduced to two small diamond-shaped lateral bars. It is narrower in *Urbanus teleus* and wider in the other species, presenting an anterior-dorsal extension as long as the tergum in *Synapte silius*.

The sterigma is the most taxonomically relevant structure of the female genitalia. This structure is modified into a tubular shape in *Pyrrhopyge charybdis charybdis* differing substantially from the other species where it, when present, has a semi-cylindrical shape. The sclerotization of the ante- and postvaginal lamellae does not occur completely in *Synapte silius*, which only presents a visible eighth sternum due to the lateral sclerotization of the antevaginal lamellae. It is completely membranous ventrally.

The surfaces and margins of the sterigma may undoubtedly serve for species level identification of several Hesperiidae. Despite lacking some details, the illustration of the sterigma in *Epargyreus clarus* (Ehrlich 1960) is clearly distinct from that in *Urbanus teleus*, where the antevaginal lamella is also present, although anteriorly separated from the postvaginal. In *Urbanus teleus*, the antevaginal lamella is directly projected ventrally under the postvaginal lamella, forming a protective structure for the ostium. Through the clarification of these structures, it is possible to visualize where one is positioned over the other, along with a small sclerotized spot (between outlines, Fig. 115), which is coincidental with the location of the orifice of the ostium in *Epargyreus clarus*.

Attention is indicated to the probable presence of a glandular structure that is adhered to the base of the sterigma, and whose function is still unknown in *Pyrgus orcus* (Fig. 112). Its exclusive and concomitant occurrence with the also exclusive large differentiated spot on the base of the valva of males of the same species (which possess a cluster of long differentiated bristles), suggests a specialization that might be related to the production, release and reception of chemical stimuli, probably of olfactory nature. Such conformation was not found in the other species, except for a membranous spot on the anterior-median region of *Urbanus teleus* (Fig. 111).

The anal papilla appear to be differentiated into two distinct sclerotization patterns, which are coincidental in *Urbanus teleus* and *Synapte silius* (Fig. 111 and 113). In the other species, they form homogenously sclerotized plates.

The bursa presents distinct shapes throughout all its length. In *Pyrrhopyge charybdis charybdis,* there seems to be a modification of the entire sterigma into a tubular shape in order to shelter the ostium at its posterior end. In *Urbanus teleus*, the orifice is posterior to the sterigma, being located in a small mid-ventral concavity of the sterigma, sheltering the ostium bursa. On the other side, the ostium of *Synapte silius* is located anteriorly-ventrally to the lateral sclerotized plates of the antevaginal lamella. The shape and position of this orifice are extremely important, because it varies even among very closely related genera, such as *Urbanus* and *Epargyreus* (Ehrlich 1960).

Synapte silius was the only species to present a certain amount of sclerotization in the duct of the bursa, which is adorned with tegumental grooves (Fig. 117). In the other species, and in the whole bursa itself, no signs of sclerotization or signa were observed. *Pyrrhopyge charybdis charybdis* exclusively presented a dilatation of the duct located on the posterior area of the corpus bursae. Unlike the other species, the body of the bursa in *Synapte teleus* is well delimited, due to the gradual constriction of the bursa towards the duct.

The observation of a sclerotized spermatophore was somewhat unexpected, as it might make it difficult to release the spermatic fluid present inside (Cordero 2005). Presumably, the presence of an opening mechanism of the spermatophore located next to the duct of the bursa, should overcome the difficult of gametes release. In *Pyrgus orcus*, the most closely related species studied herein, this structure is entirely membranous. The great difficulty in finding specimens presenting this structure makes it difficult to perform comparative studies. Therefore, it would be necessary to acquire better information about the reproductive behavior of the species, in order to make any inferences about some of its morphological structures.

Conclusions

Despite seldom being used by taxonomists within the Hesperiidae, several characters of the thorax and abdomen can be added to those already discovered. Among them, the following can be mentioned: the presence and development of the cervical organ; the shape and/or sclerotization spots of the pronotum; the dorsal apophyses of the lateral plate of the pronotum and the spina I; the location of the insertion orifice of the tegulae; the development of the anepisternum; the presence, shape and/or extension of the pre-coxal, marginopleural, and preepimeral sutures on the meso- and metathorax; the first tergum; the pre- and postspiracular bars; the last pre-genital segment; and the entire conformation of the genitalia, both of males and females. Likewise, several characters located on the appendices themselves are not completely known and vary significantly amongst the species examined, such as: the presence of a differentiated triangular dorsal sclerite of the epimeron II; the number of apical bristles on the last tarsomere; the shape of the arolium and tarsal claws on the legs; and the degree of sclerotization of the dcs vein on the fore wing. Additionally, there are also strong taxonomic characters that are usually mentioned in the literature and corroborated by the present study, related to the species examined, such as: the number of tibial spurs; the size of the discal cell; the presence of the costal crease and of the recurring M vein; and the location of the base of the M2 vein. The extension of the dcs and of the 3A veins on the fore wing and of the dcu on the hind wing, indicated as sexually dimorphic within the mentioned species, is a character not previously mentioned in the literature. The presence of the costal vein in both wings contradicts most of the morphological studies and illustrations of other Lepidoptera species, where it is not usually present or illustrated. Its usage still deserves new studies in order to attest its real absence in any of its subgroups.

Furthermore, we emphasize the need for more detailed studies regarding the function and/or development of certain organs or structures that have seldom been mentioned in the literature, such as: the cervical organ, the metathoracic glandular apophysis, the hook-shaped recess of the epimeron III, the wing coupling mechanism itself along with the differentiated scales attached to it, and the costal vein on the hind wing. Chemical and behavioral studies are necessary to complement this type of information.

Acknowledgments

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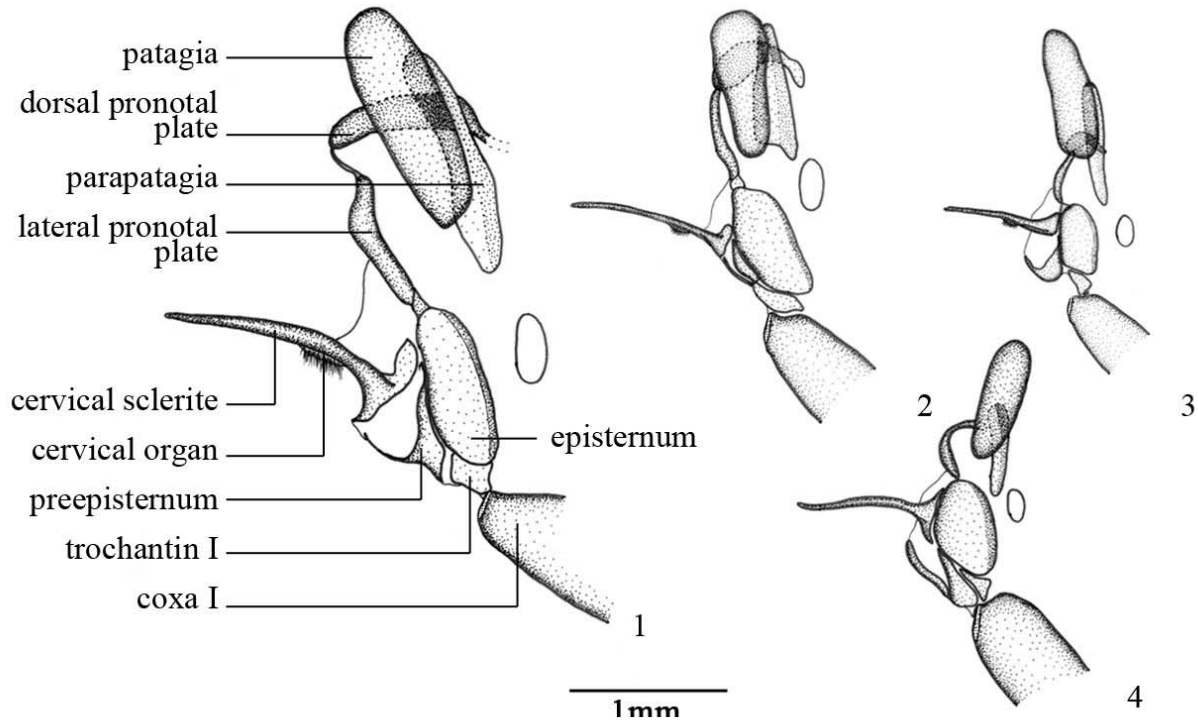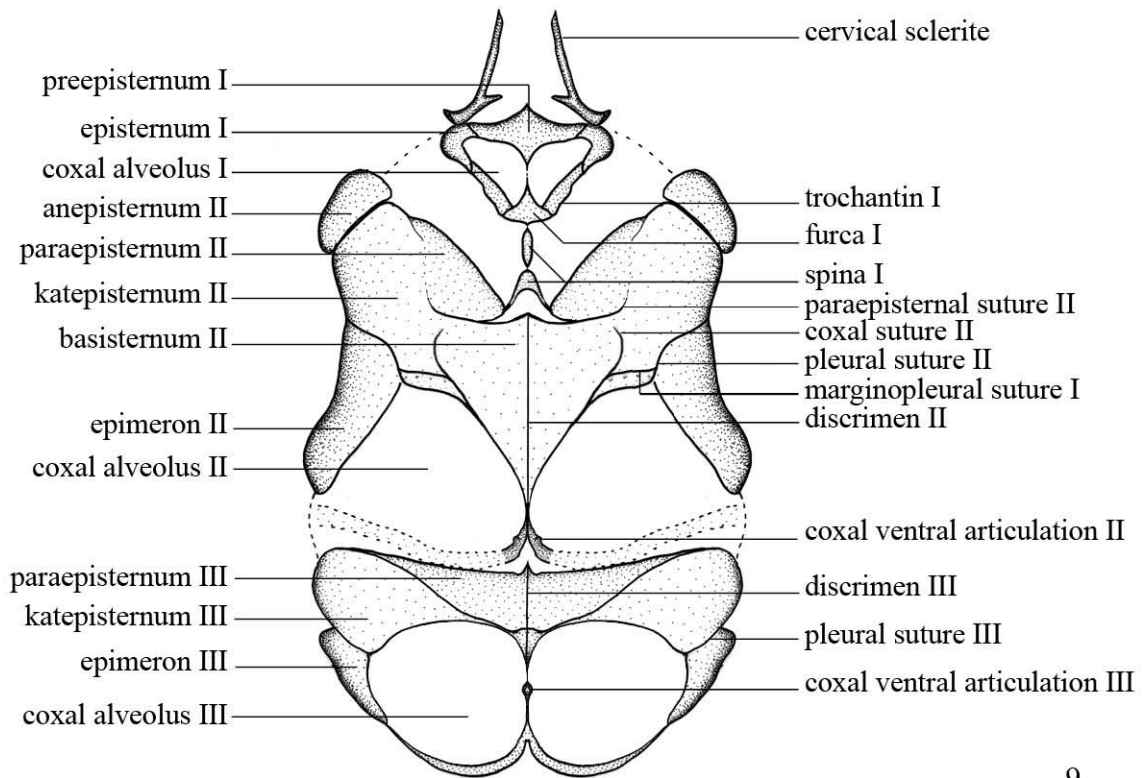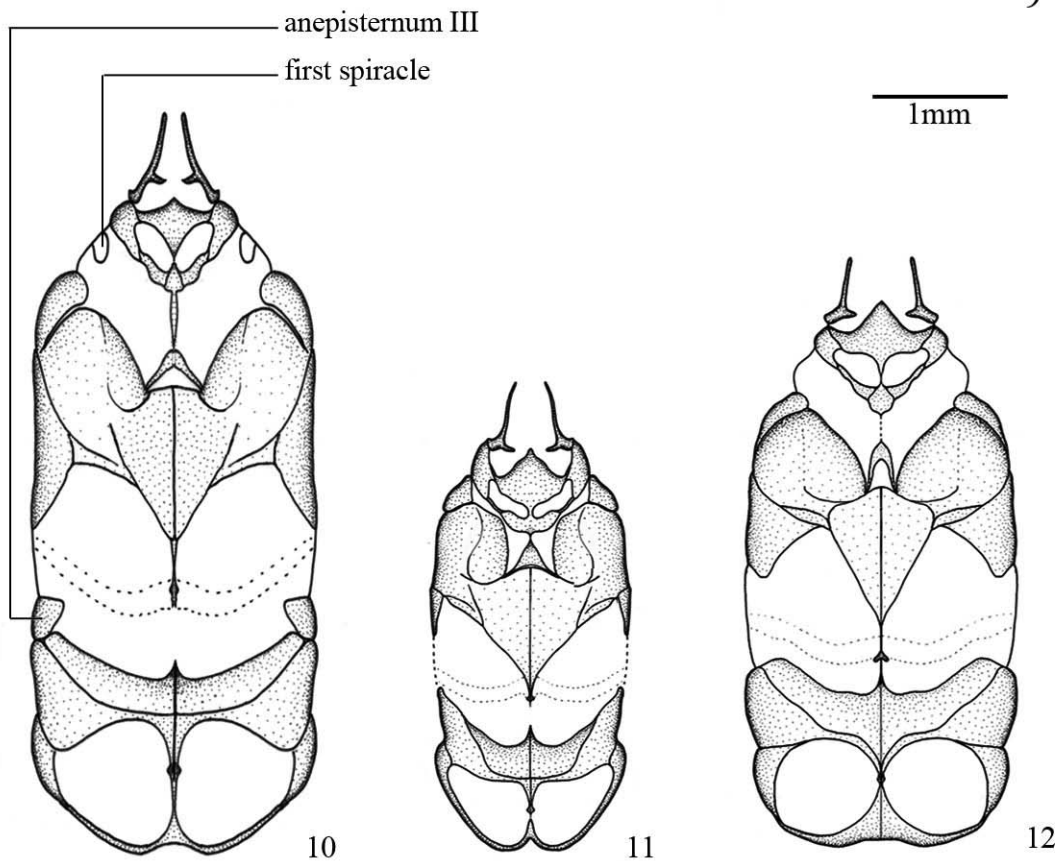
Figures 1-4. Lateral view of cervical sclerite and prothorax. **1)** *Pyrrhopyge charybdis charybdis*; **2)** *Urbanus teleus*; **3)** *Pyrgus orcus*; **4)** *Synapte silius*.
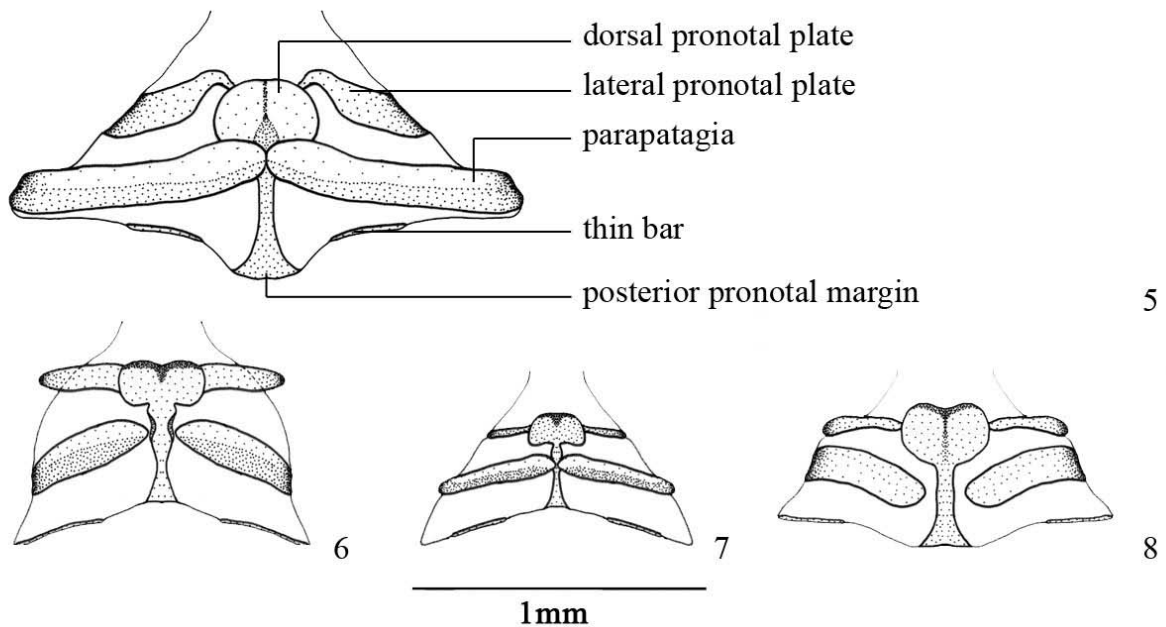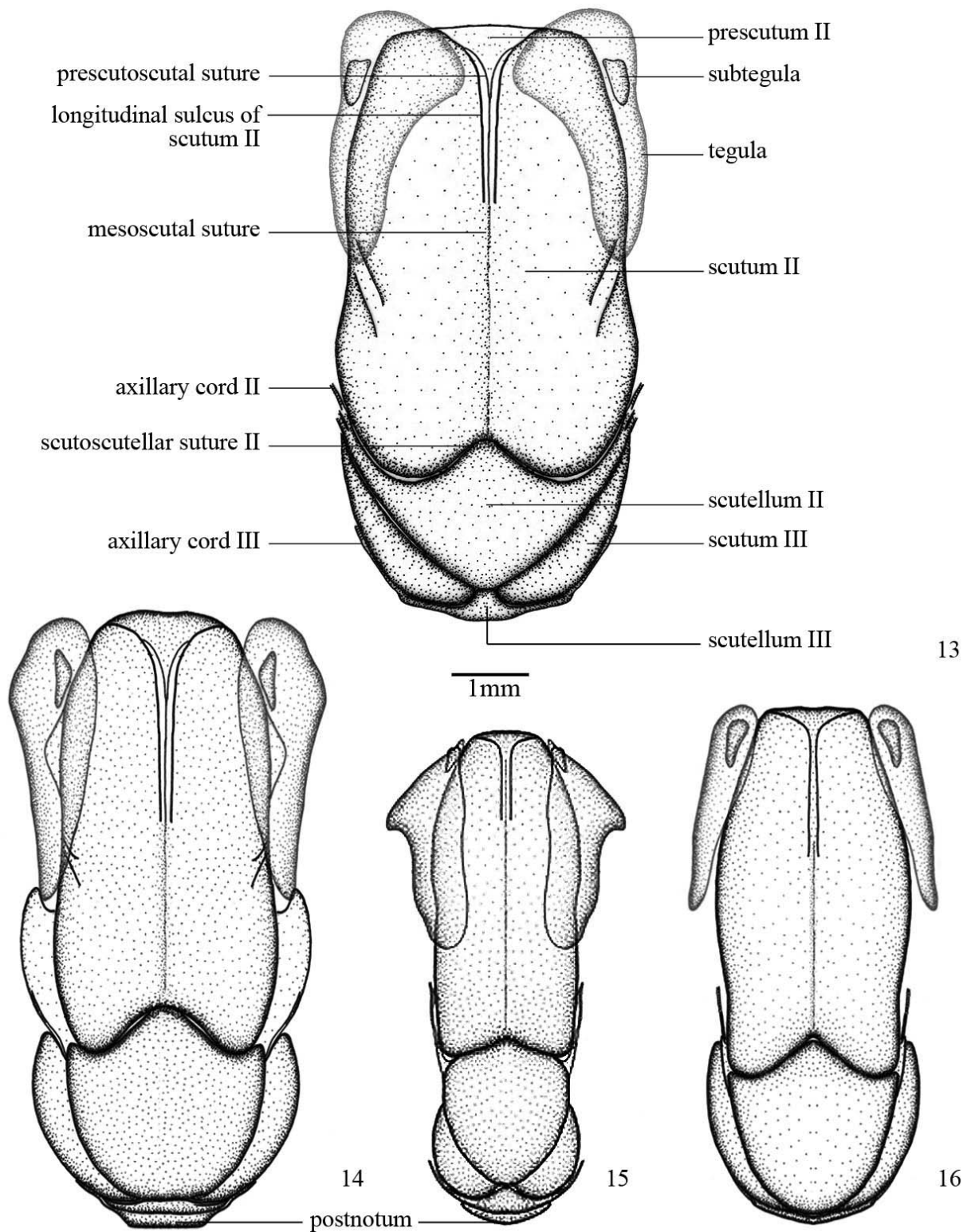

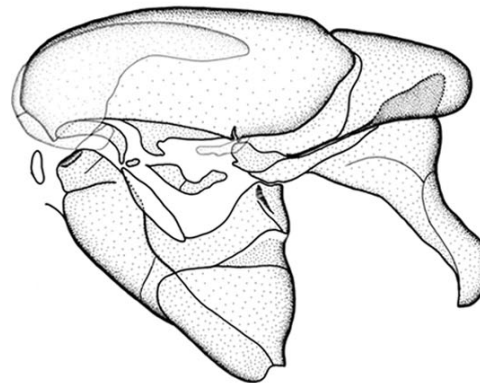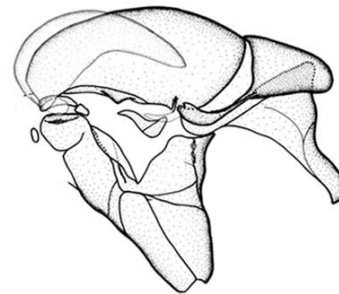**Figures 5-8**. Dorsal view of prothorax. **5)** *Pyrrhopyge charybdis charybdis*; **6)** *Urbanus teleus*; **7)** *Pyrgus orcus*; **8)** *Synapte silius*.
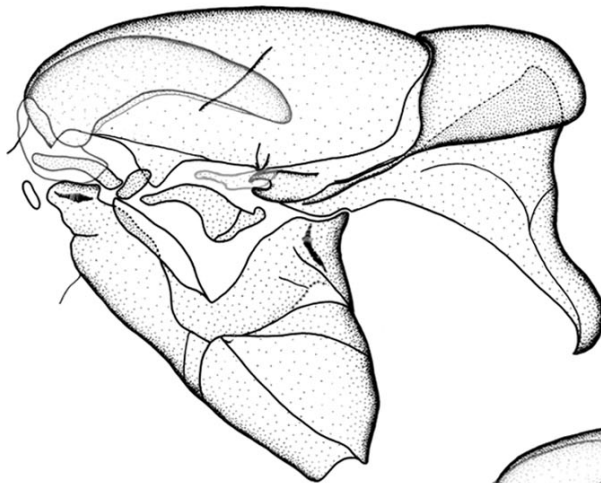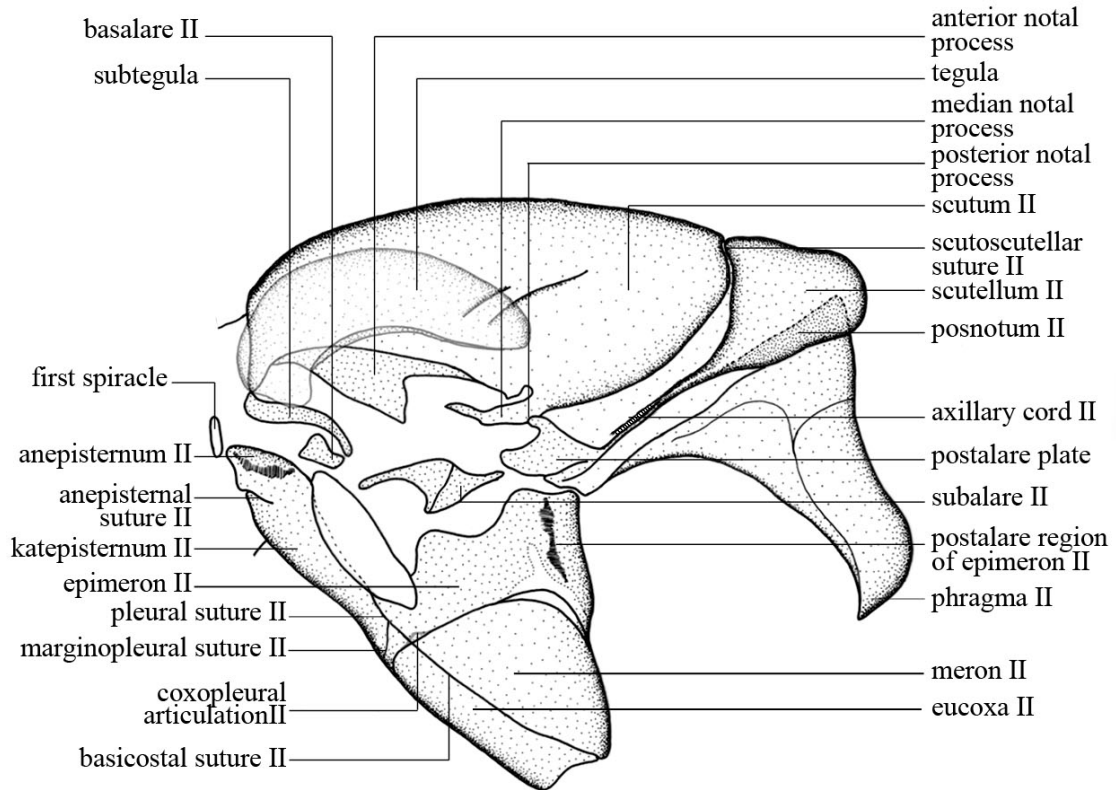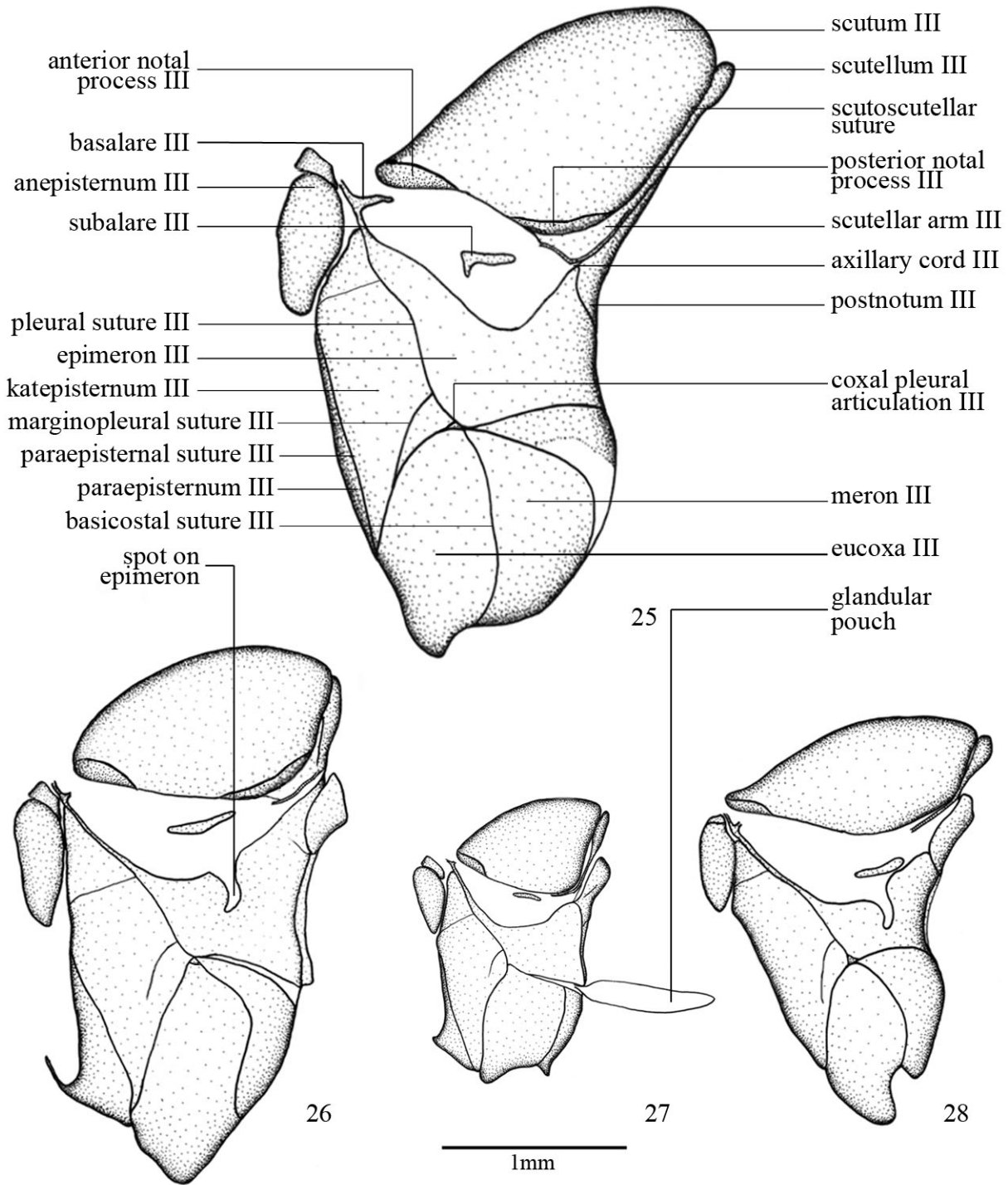
cervical sclerite

preepisternum I

episternum I

coxal alveolus I

anepisternum II

paraepisternum II

katepisternum II

basisternum II

epimeron II

coxal alveolus II

trochantin I

furca I

spina I

paraepisternal suture II

coxal suture II

pleural suture II

marginopleural suture I

discrimen II

coxal ventral articulation II

paraepisternum III

katepisternum III

epimeron III

coxal alveolus III

discrimen III

pleural suture III

coxal ventral articulation III

9

anepisternum III

first spiracle

1mm

10

11

12

Figures 9-12. Ventral view of cervix and thorax. **9)** *Pyrrhopyge charybdis charybdis*; **10)** *Urbanus teleus*; **11)** *Pyrgus orcus*; **12)** *Synapte silius*.

Figures 13-16. Dorsal view of mesothorax and metathorax. **13)** *Pyrrhopyge charybdis charybdis*; **14)** *Urbanus teleus*; **15)** *Pyrgus orcus*; **16)** *Synapte silius*.

basalare II

subtegula

anterior notal process

tegula

median notal process

posterior notal process

scutum II

scutoscutellar suture II

scutellum II

posnotum II

first spiracle

anepisternum II

anepisternal suture II

katepisternum II

epimeron II

pleural suture II

marginopleural suture II

coxopleural articulationII

basicostal suture II

axillary cord II

postalare plate

subalare II

postalare region of epimeron II

phragma II

meron II

eucoxa II

17

18

19

1mm

20

Figures 17-20. Lateral view of mesothorax. **17)** *Pyrrhopyge charybdis charybdis*; **18)** *Urbanus teleus*; **19)** *Pyrgus orcus*; **20)** *Synapte silius*.
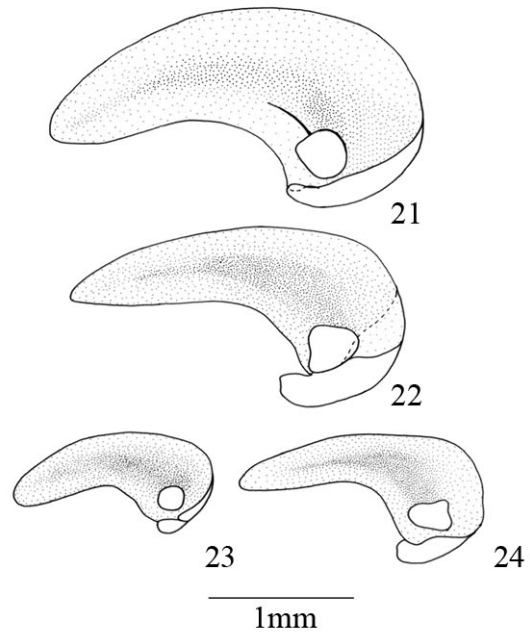
Figures 21-24. Lateral view of internal surface of tegula. **21)** *Pyrrhopyge charybdis charybdis*; **22)** *Urbanus teleus*; **23)** *Pyrgus orcus*; **24)** *Synapte silius*.

scutum III

scutellum III

scutoscutellar suture

anterior notal process III

posterior notal process III

basalare III

anepisternum III

scutellar arm III

subalare III

axillary cord III

postnotum III

pleural suture III

epimeron III

katepisternum III

coxal pleural articulation III

marginopleural suture III

paraepisternal suture III

paraepisternum III

meron III

basicostal suture III

eucoxa III

spot on epimeron

glandular pouch

25

26

27

28

1mm

Figures 25-28. Lateral view of metathorax. **25)** *Pyrrhopyge charybdis charybdis*; **26)** *Urbanus teleus*; **27)** *Pyrgus orcus*; **28)** *Synapte silius*.
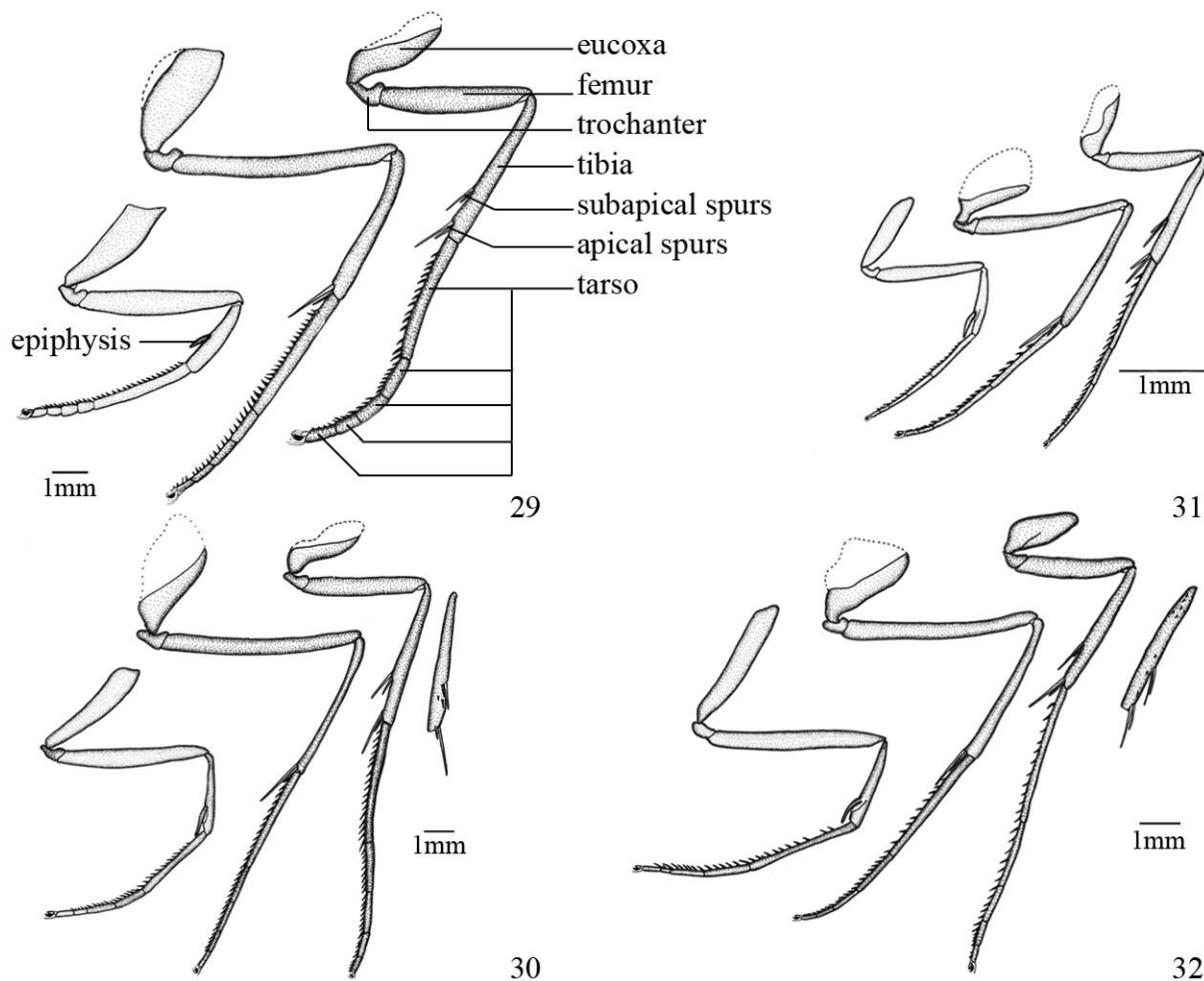
Figures 29-32: Internal surface of prothoracic, mesothoracic and metathoracic legs (left to right). **29)** *Pyrrhopyge charybdis charybdis*; **30)** *Urbanus teleus**; **31)** *Pyrgus orcus*; **32)** *Synapte silius**. *External surface illustrated.
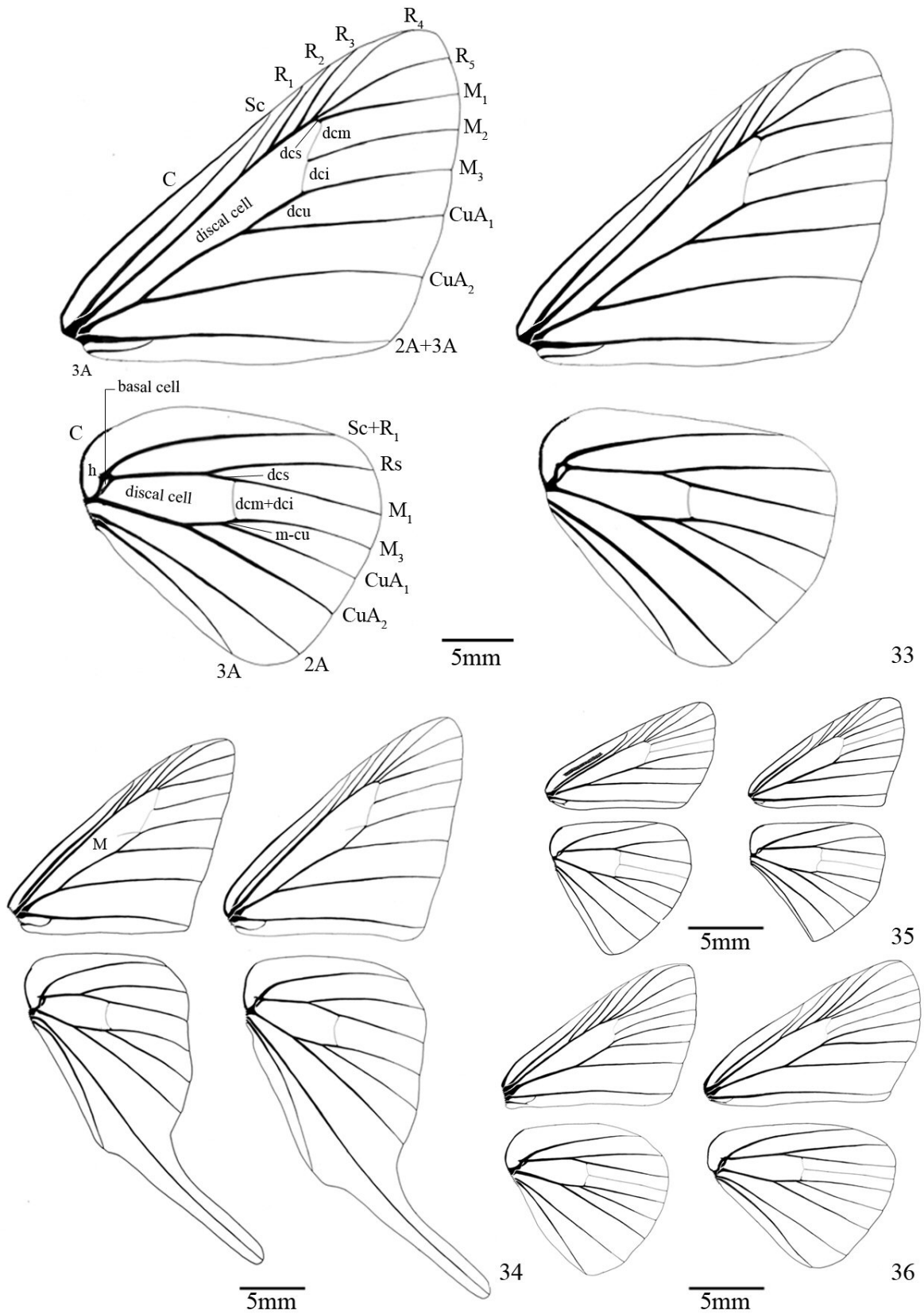
Figures 33-36. Dorsal view of clarified mesothoracic and metathoracic wings of males (left) and females (right). **33)** *Pyrrhopyge charybdis charybdis*; **34)** *Urbanus teleus*; **35)** *Pyrgus orcus*; **36)** *Synapte silius*.
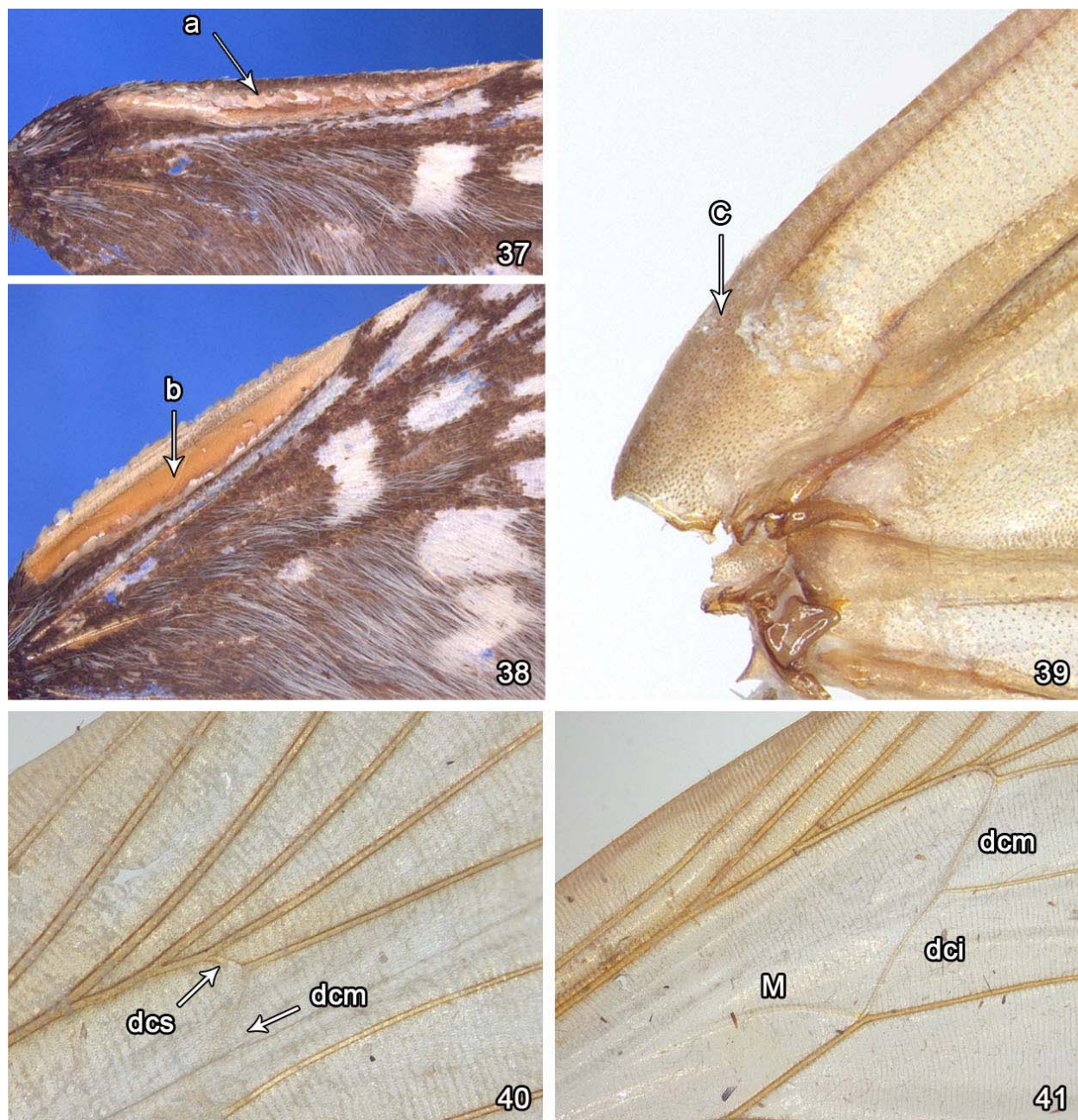
Figures 37- 41. Details of wings of some observed Hesperiidae. **37, 38)** *Pyrgus orcus*; **39, 40)** *Synapte silius*; **41)** *Urbanus teleus*. a. costal fold; b. costal fold without protection scales (Barth 1960); other letters refer to vein terminology.
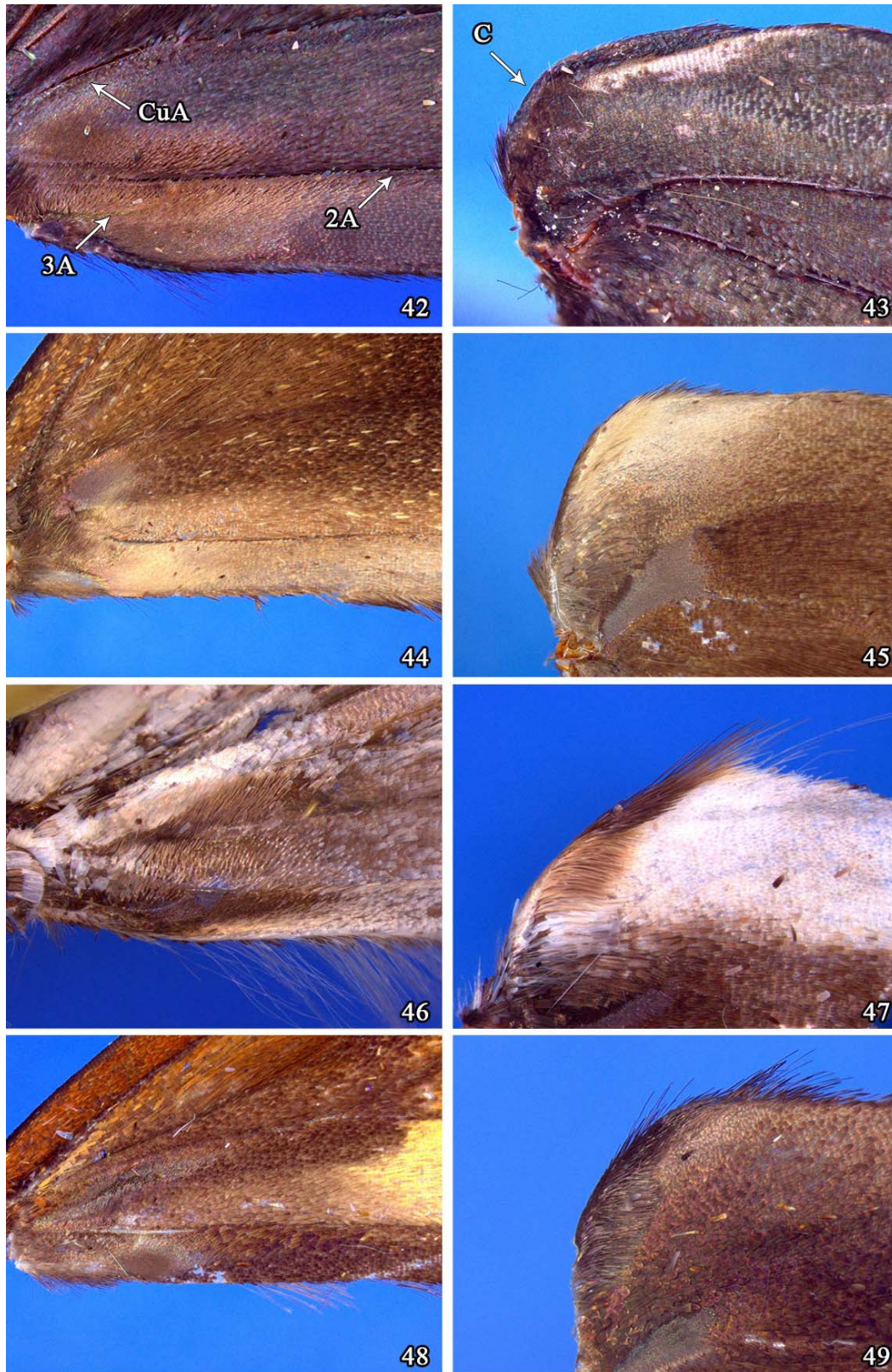
Figures 42- 49. Details of wing-coupling mechanism viewed on ventral mesothoracic wingbase (left) and dorsal metathoracic wingbase (right). **42, 43)** *Pyrrhopyge charybdis charybdis*; **44, 45)** *Urbanus teleus*; **46, 47)** *Pyrgus orcus*; **48, 49)** *Synapte silius*.
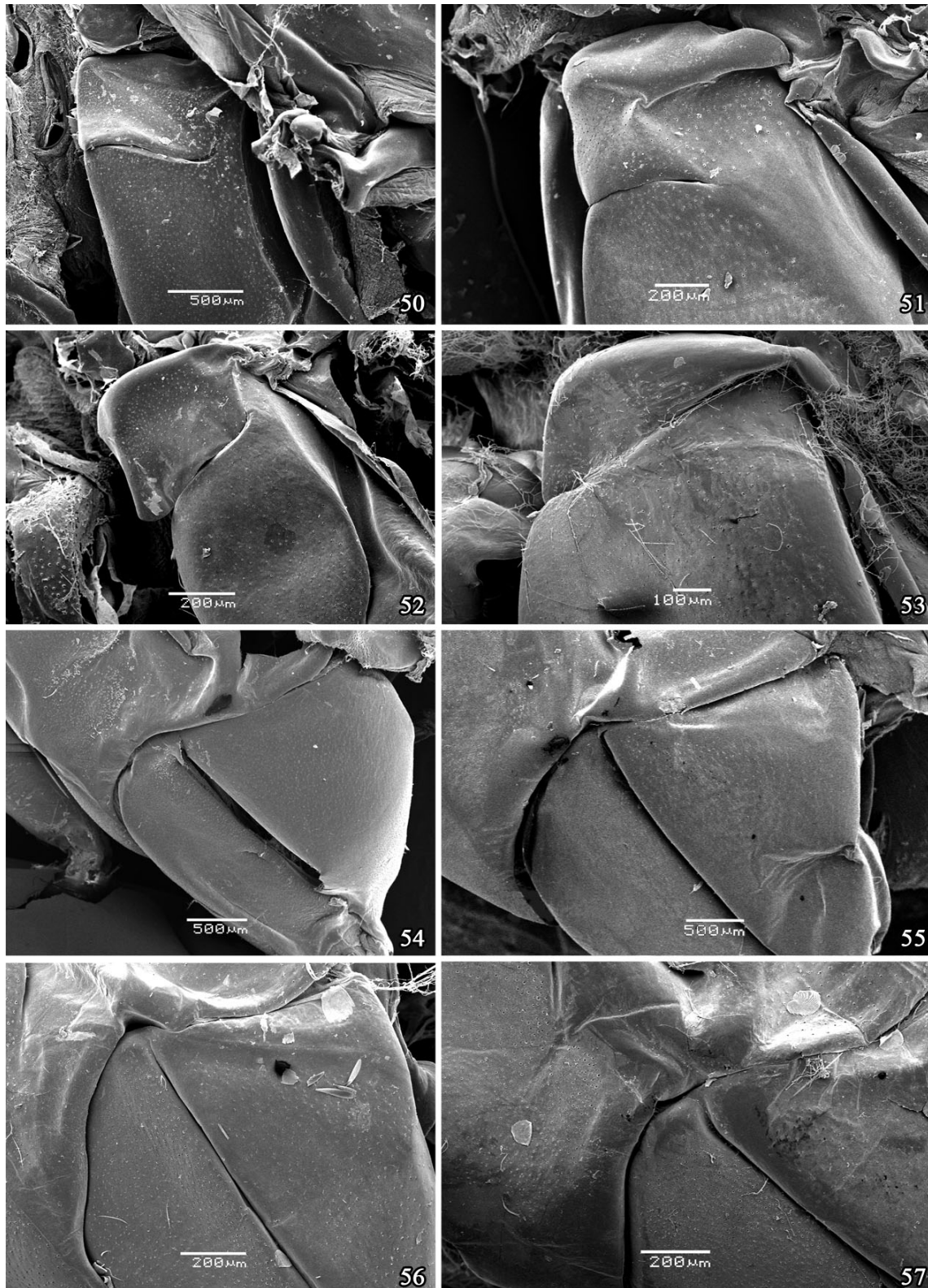
Figures 50- 57. Lateral view of anepisternum II (Fig. 50 to 53) and coxopleural articulation II (Fig. 54 to 57). **50, 54)** Pyrrhopyge charybdis charybdis; **51, 55)** Urbanus teleus; **52, 56)** *Pyrgus orcus*; **53, 57)** *Synapte silius*.
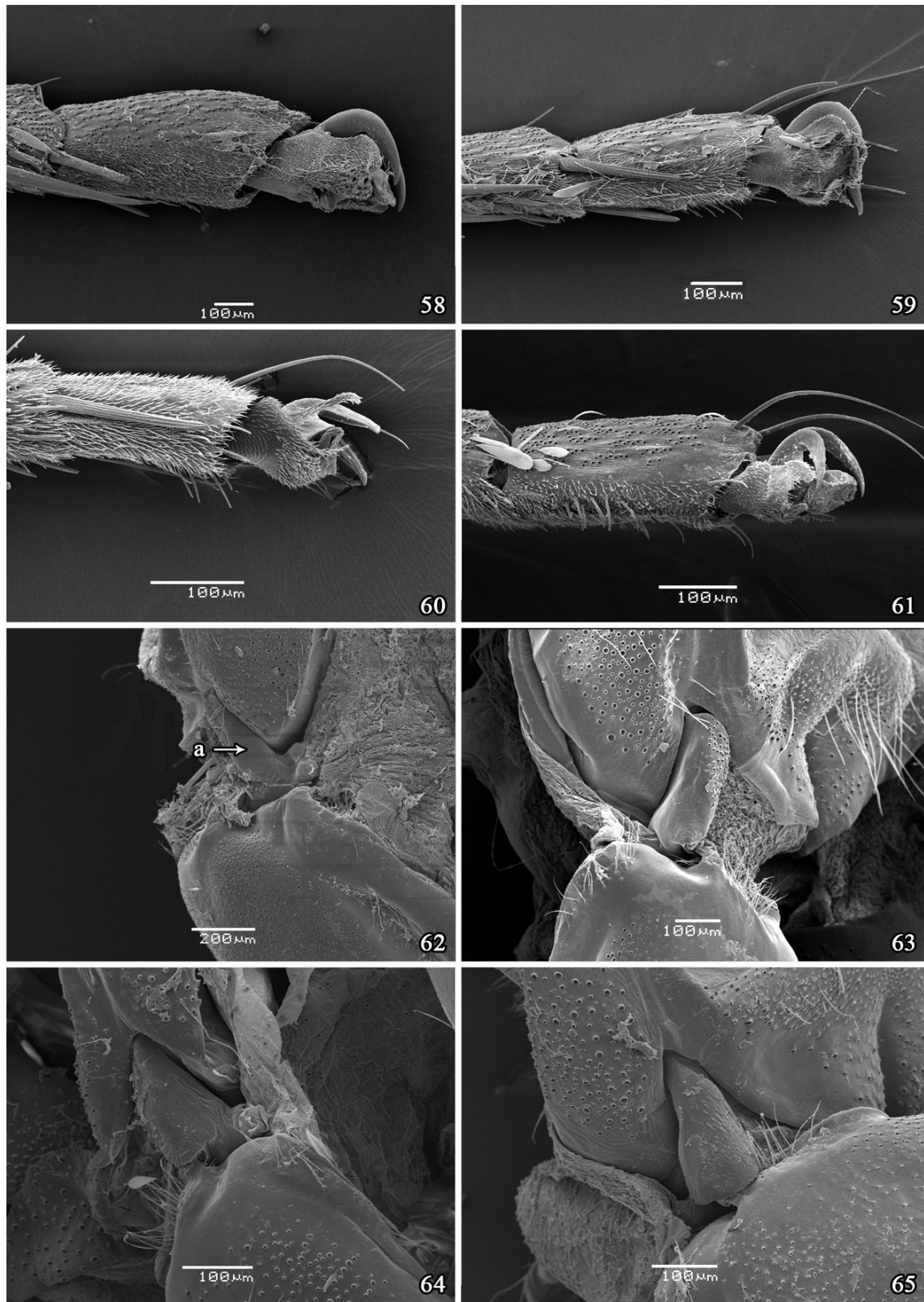
Figures 58- 65. Lateral view of last tarsomere and pretarsum I (Fig. 58 to 61), and trochantin I (Fig. 62 to 65). **58, 62)** *Pyrrhopyge charybdis charybdis*; **59, 63)** *Urbanus teleus*; **60, 64)** *Pyrgus orcus*; **61, 65)** *Synapte silius*. a: trochantin I.
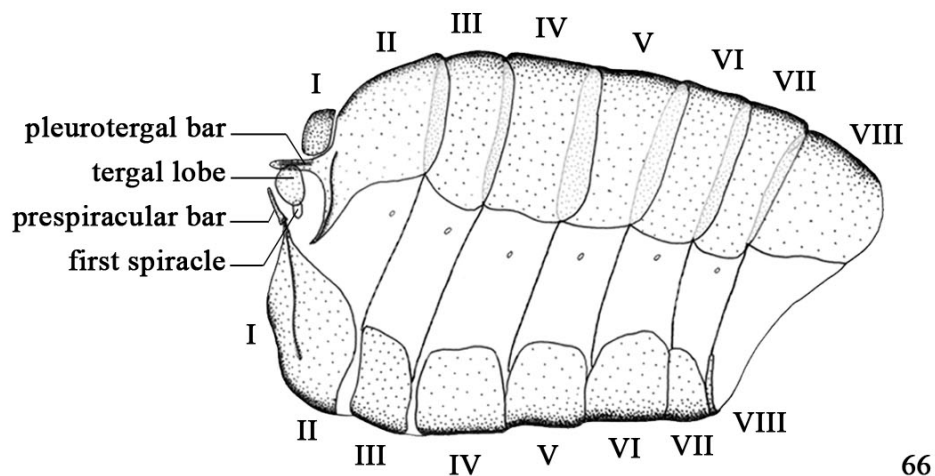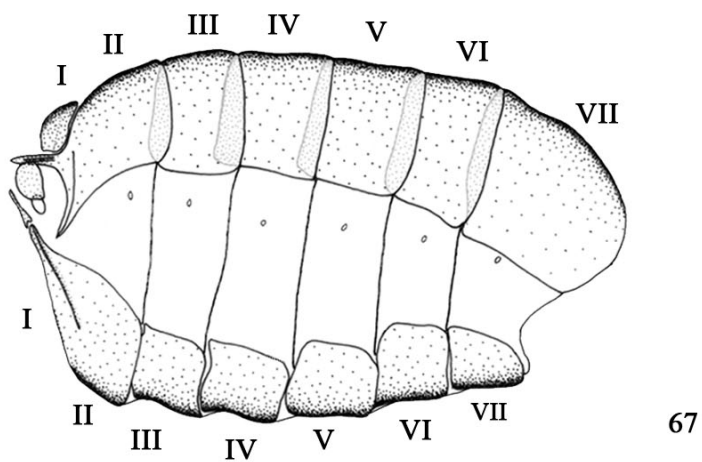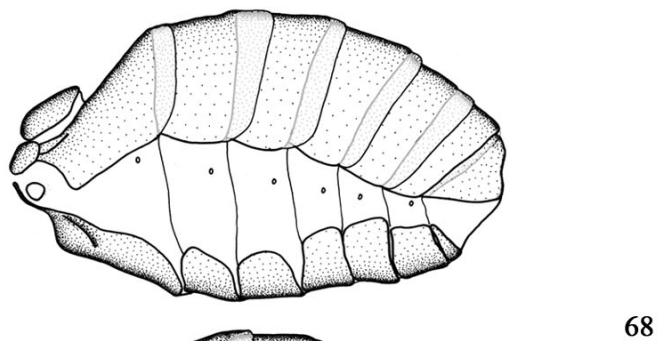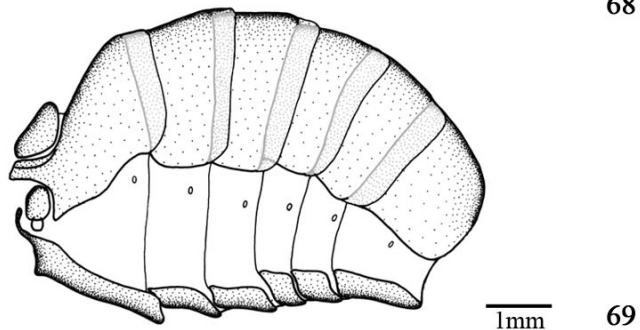
Figures 66-69. Lateral view of male (Fig. 66 and 68) and female (Fig. 67 and 69) abdomens. **66, 67)** *Pyrrhopyge charybdis charybdis*; **68, 69)** *Urbanus teleus*.
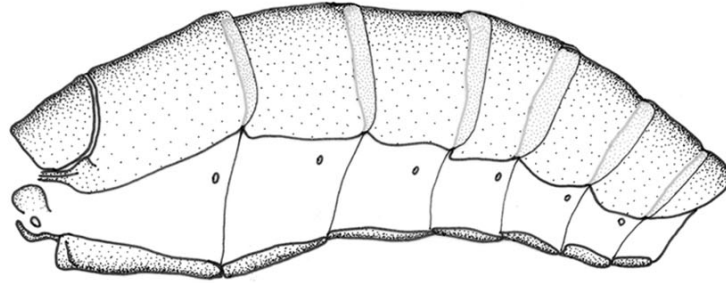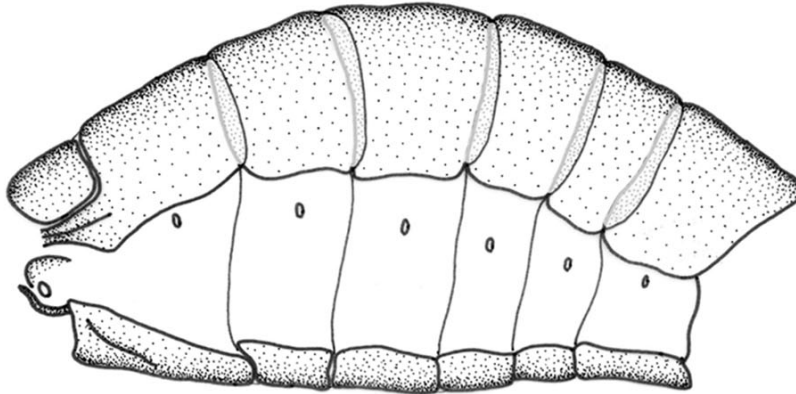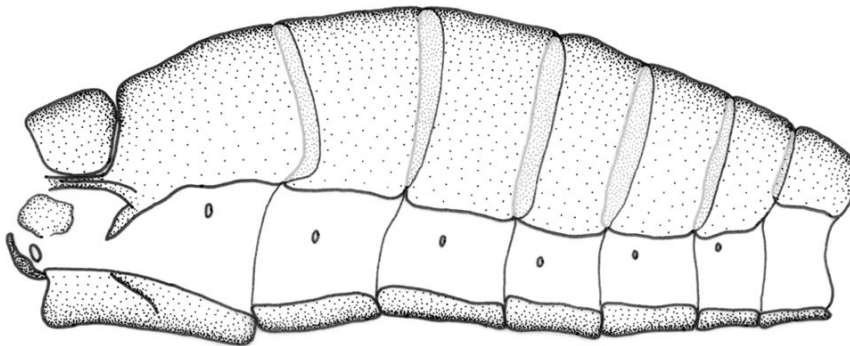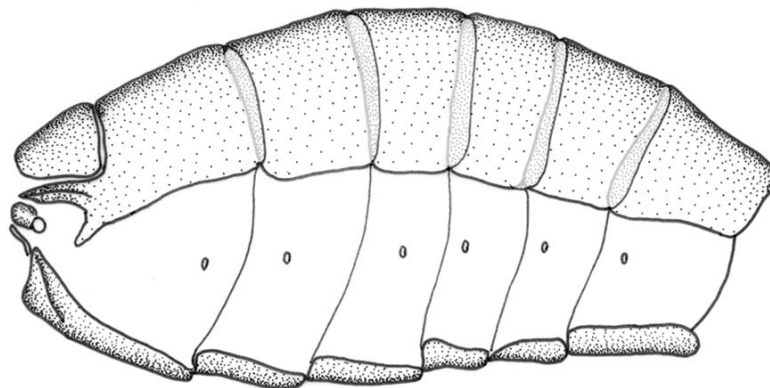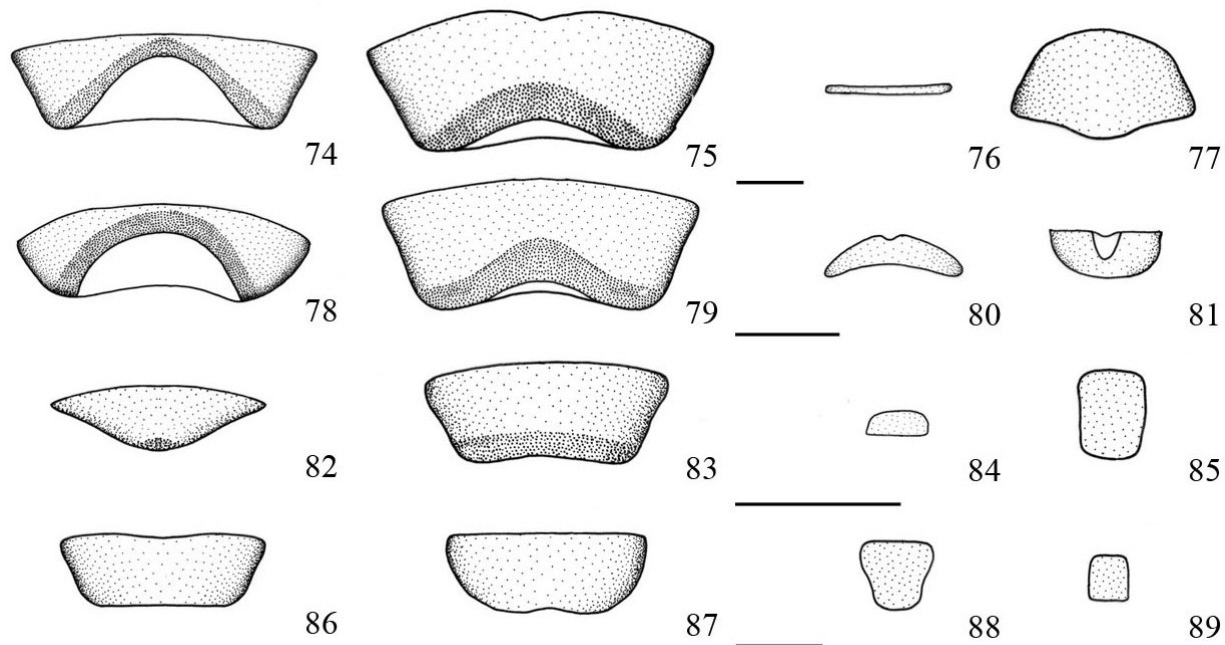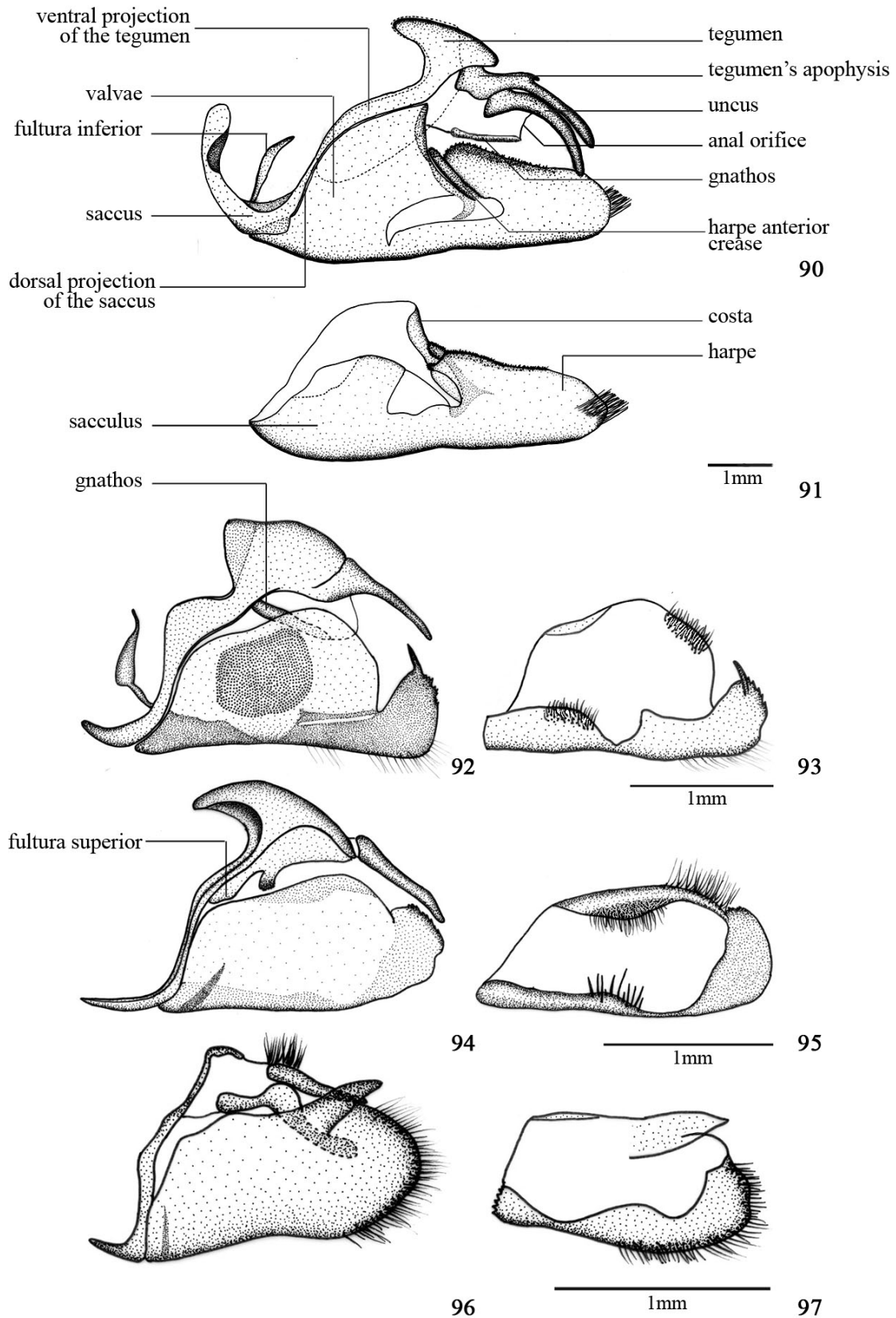
Figures 70-73. Lateral view of male (Fig. 70, 72) and female (Fig. 71, 73) abdomens. **70, 71)** *Pyrgus orcus*; **72, 73)** *Synapte silius*.

Figures 74-89. Dorsal view from last tergum (two left columns) and ventral view from sternum (two right columns): **74 to 77)** *Pyrrhopyge charybdis charybdis*; **78 to 81)** *Urbanus teleus*; **82 to 85)** *Pyrgus orcus*; **86 to 89)** *Synapte silius*.
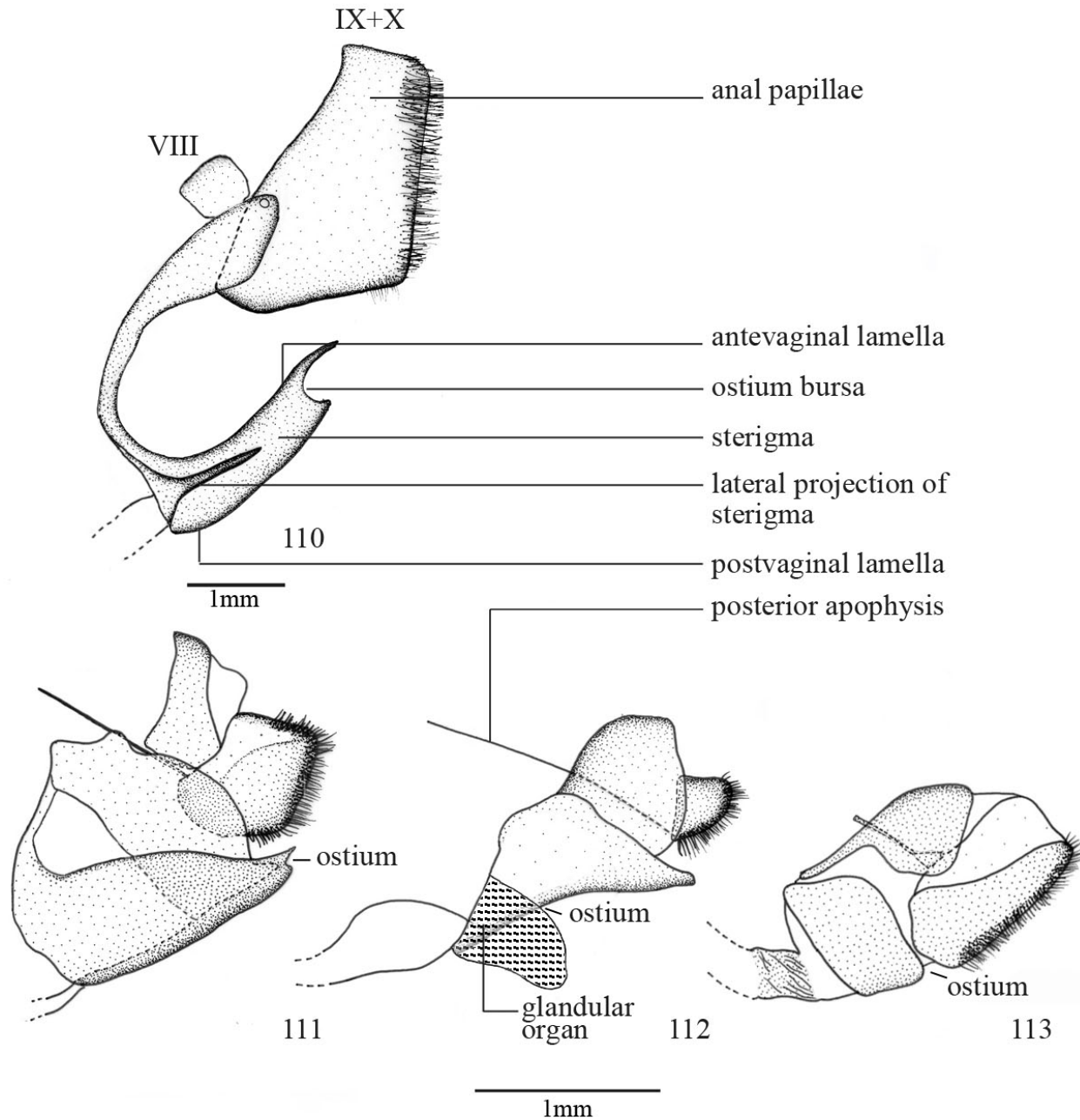
Figures 90-97. Lateral view of external surface of male genitalia (left), and internal surface of valvae (right). **90, 91)** *Pyrrhopyge charybdis charybdis*; **92, 93)** *Urbanus teleus*; **94, 95)** *Pyrgus orcus*; **96, 97)** *Synapte silius*.
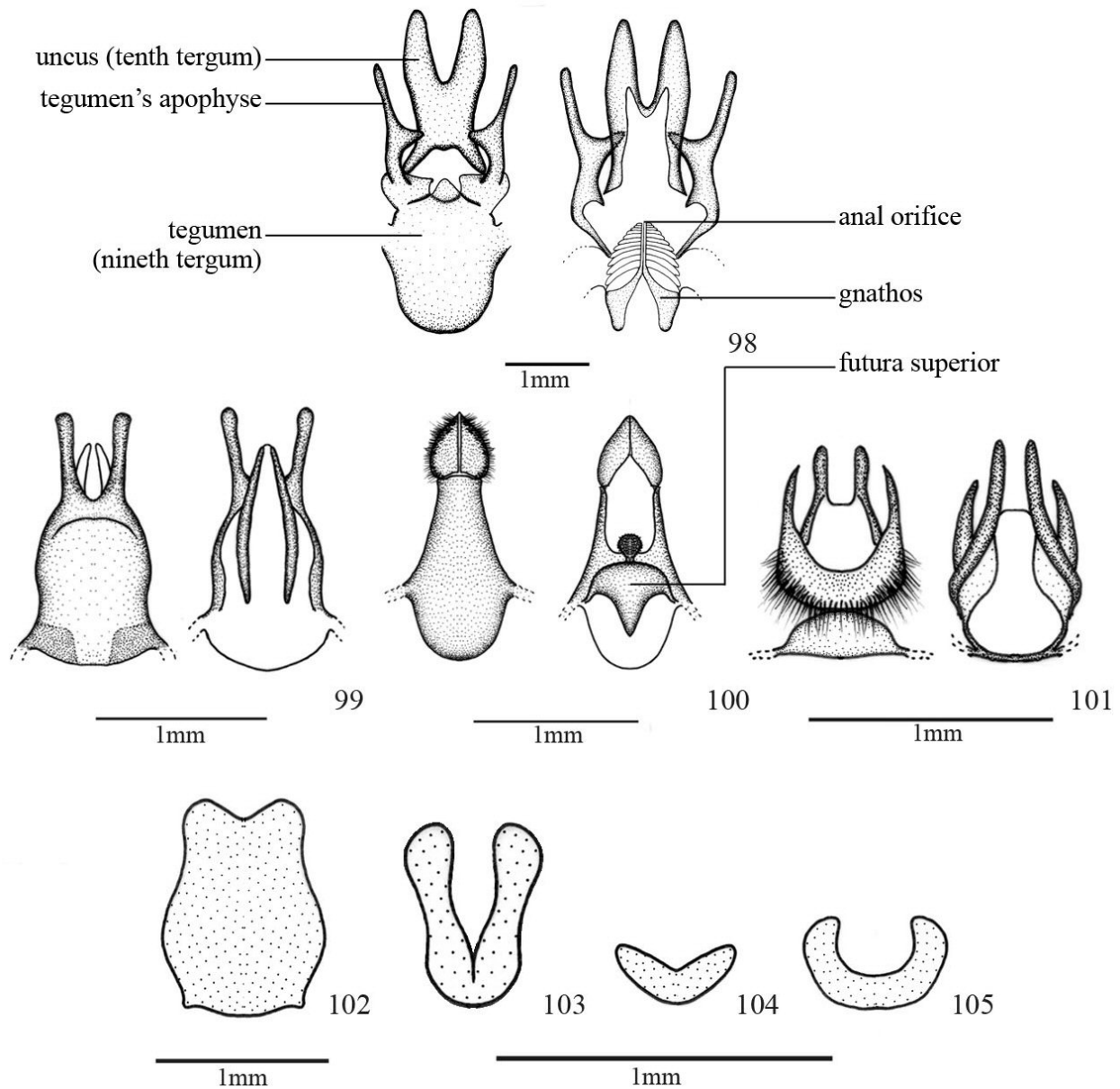
Figures 98-105. Dorsal (left) and ventral (right) view of ninth and tenth tergum of male genitalia. **98)** *Pyrrhopyge charybdis charybdis*; **99)** *Urbanus teleus*; **100)** *Pyrgus orcus*; **101)** *Synapte silius*. **102-105**. Posterior view of futura inferior. **102)** *Pyrrhopyge charybdis charybdis*; **103)** *Urbanus teleus*; **104)** *Pyrgus orcus*; **105)** *Synapte silius*.
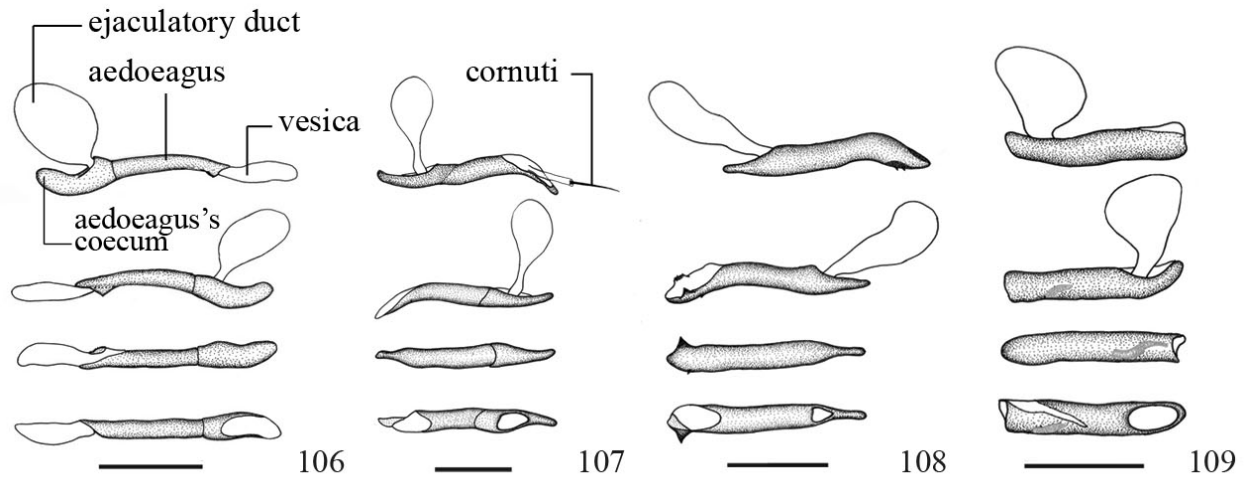
Figures 106-109. Different views of the penis: left lateral, right lateral, ventral and dorsal views (top to bottom). **106)** *Pyrrhopyge charybdis charybdis*; **107)** *Urbanus teleus*; **108)** *Pyrgus orcus*; **109)** *Synapte silius*.

IX+X

anal papillae

VIII

antevaginal lamella

ostium bursa

sterigma

lateral projection of
sterigma

110

postvaginal lamella

posterior apophysis

1mm

ostium

ostium

glandular
organ

ostium

111   112   113

1mm

Figures 110-113. Lateral view of eighth, ninth and tenth segments which form the female genitalia **110)** *Pyrrhopyge charybdis charybdis*; **111)** *Urbanus teleus*; **112)** *Pyrgus orcus*; **113)** *Synapte silius*.
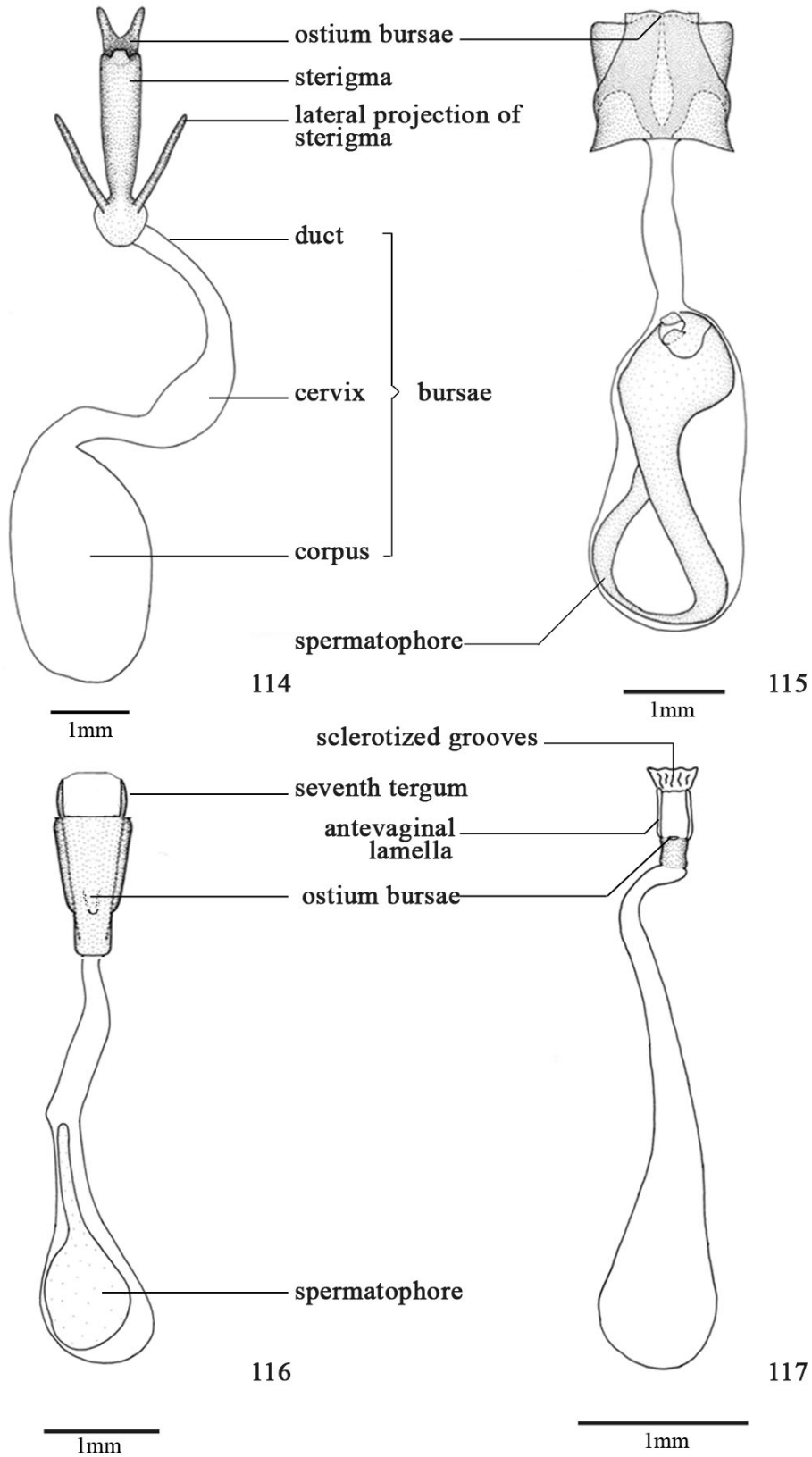
Figures 114-117. Ventral view of female genitalia. **114)** *Pyrrhopyge charybdis charybdis*; **115)** *Urbanus teleus*; **116)** *Pyrgus orcus*; **117)** *Synapte silius*.